Cunninghamia lanceolata (CHINESE FIR).

A STUDY OF ITS POTENTIAL AS A COMMERCIAL PLANTATION SPECIES IN NEW ZEALAND

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ABSTRACT

Cunninghamia lanceolata (Lamb.) Hook. (Chinese fir) is an evergreen conifer occurring naturally in the sub-tropical region of central - southern China. *C. lanceolata* is considered one of the most important trees in China, in terms of areas of planting, timber production and timber usage; it has been cultivated as a timber species for over 1000 years and as such its silviculture is well developed.

The species has not been planted (commercially) much outside China and Taiwan. The aim of this thesis was to provide, by way of physiological and genetic experiments (of seedlings) on a variety of provenances, information on the prospects for growing *C. lanceolata* as a commercial forest tree species in New Zealand. Additional factors such as growth pattern and habit, wood properties, palatability to opossums, and climate modelling were also examined.

Provenance differences, while reported in the literature, were not so apparent in this study. Isozyme analysis of seed from eight of the eleven seedlots used in this study showed low levels of variability both as a species and between provenances, while a nursery trial did not produce any significant differences in terms of second year height growth or bud burst. However, length of growing season as evidenced by date of bud set did show some variation; with bud set being strongly correlated with latitude, mean annual temperature, mean temperature of the coldest month, and temperature sum. Similarly in the requirement of winter chilling in order to promote bud burst a north-south trend was apparent, as with the nursery trial, with northern provenances bursting fewer buds when little or no chilling was received. For the purposes of this study, however, the only observed difference which is important is the degree of bud set at the end of the growing season, with the closely correlated degree of frost damage. Northern provenances which set bud earlier are therefore better suited to New Zealand conditions.

Growth of *C. lanceolata* responded greatly to temperature: Significant differences were seen between low and high day temperatures, with greatest growth at 28 ^{o}C. This is closely related to temperatures during its growth period in China; there, rapid growth occurs between June and September when mean monthly temperatures range from about 22 to 30 ^{o}C. There are few sites in New Zealand which have mean monthly temperatures this high over summer.

Winter frost resistance was found to be adequate for most New Zealand sites and compares favourably with New Zealand podocarps and *P. radiata*. Hardiness values

were -15.5 to -15.9 °C. Conversely however, *C. lanceolata* was very susceptible to out of season frosts; a heavy frost of -5 °C resulted in 100 % mortality. Lighter frosts in autumn (*ca.* -0.5 to -3.5 °C) killed growing tips of seedlings that had not set bud. In choosing sites for the species, out of season frosts are likely to be a major limiting factor.

Water requirements were high; new leaf growth was almost 50 % higher for unstressed seedlings (100 % field capacity) than for stressed seedlings (30 and 15 % field capacity). Mortality was also greater at the lowest water level although tolerance to low levels can be developed in well established seedlings at the expense of growth. Recovery of stressed seedlings was apparent after two weeks of rewatering to field capacity; however rates of photosynthesis were still significantly lower than those of unstressed seedlings and conversely stomatal resistance was greater. This suggests that long term (morphological) change had occurred in stressed seedlings.

The nutrient experiment showed that nutrient deficiencies and poor growth occurred in seedlings grown at low nutrient levels. Greatest growth was found at high levels compared with other tree species, and tissue analysis also revealed comparatively high levels of foliar concentrations. There was evidence of mycorrhizal colonization resulting in greater seedling growth compared to seedlings that were non-mycorrhizal. However the response was less significant than overall nutrient status and was only apparent at high nutrient levels. Thus the species has a requirement for fertile soils and application of fertilisers.

Temperature affected photosynthesis more than did light intensity. At 20 °C light saturation was approached at approximately one third of full sunlight (640 μE) while at 28 °C the response curve was still increasing. Light compensation point was low (20 μE) compared to *P. radiata* (39 μE). Seedling appearance was also greener when grown under 30 % shade cloth as opposed to full sunlight where seedlings appeared yellowed. This and studies on mixed stands and *C. lanceolata*'s ecology suggest that the species prefers weak sunlight or low light intensities.

Other experiments examined the growth pattern and habit of *C. lanceolata*. The species has a definite seasonal pattern of shoot growth; following bud burst in early September growth was typically sigmoid, slowing down and ceasing around April when buds were set. Small sized resting buds were formed over winter; no height growth occurred from May through to August (winter) until early September when buds began to swell and burst again. The growing season in New Zealand was approximately 8 months, the small size of the bud suggested that predetermined growth was only a minor part of the total season's growth and free growth must therefore follow. Estimation of seasonal shoot growth in mature (25 year old) trees indicated that less than half of a season's shoot growth was predetermined. Free growth allows *C. lanceolata* to maximise potential

growing conditions while the predetermined component acts as a buffer against unfavourable years.

Seedlings grown under an 8 hour daylength did not show any difference in growth to those under natural summer daylengths, and there was no sign of bud formation: However seedlings under high day (22 and 24 ^{o}C) and low night (9 and 7 ^{o}C) temperatures, and long (16 hour) photoperiod showed signs of dormancy after one month. Most seedlings had formed terminal resting buds and had adopted a brown winter colouration. Low night temperatures of 9 ^{o}C or less were therefore primarily responsible for bud set. *C. lanceolata* did not exhibit true dormancy in the sense that chilling was required before growth could resume under favourable conditions. However chilling did significantly hasten bud burst. Provenance differences were noticed when no chilling or very light chilling was applied; however after long periods of chilling all provenances burst bud more or less immediately. This suggests that under natural New Zealand conditions rapid bud burst would occur in all provenances.

In addition to defining the species' requirements for (successful) growth, the presence of one 58-year-old stand in New Plymouth and two 25-year-old plots in Rotorua enabled a preliminary study on wood properties to be made. Basic densities were lower than much of the native grown (Chinese) *C. lanceolata* and considerably lower than the range for *P. radiata* in New Zealand. The low basic density resulted in lower strength values for mechanical properties (bending, compression, shear tests). Drying rates were very similar to *P. radiata* and air drying or drying under a conventional (high temperature) *P. radiata* kiln schedule produce very little degrade. The low strength and basic density of the timber makes *C. lanceolata* less suitable for structural uses compared with *P. radiata*, and more suited to end uses where strength is not important.

Browse damage from opossums was also examined. Pen trials showed that there was a marked preference for *P. radiata* over *C. lanceolata* seedlings in the short term. However once *P. radiata* seedlings were eaten, *C. lanceolata* seedlings were then completely stripped over two nights. This suggests that damage at establishment may not initially be a problem, but that once opossums are familiar with *C. lanceolata* as a food source, damage may well increase.

Global modelling using the WORLD program developed by Dr Trevor Booth showed a variety of countries as suitable for *C. lanceolata*, including those where the species has been planted and trialed. New Zealand sites were considered suitable when both uniform and winter rainfall distributions were included as parameters. A more detailed model for New Zealand developed by Dr Neil Mitchell was next used to identify specific areas. Results showed that *C. lanceolata* was climatically suited to a restricted range of sites, almost exclusively in the North Island.

The experimental findings suggest that while New Zealand conditions may not be optimal for growth, the species nevertheless has (limited) prospects for establishment in New Zealand. Provenance differences in growth were not found at the early seedling stage of growth; however selection of provenances in terms of short growing season may be advantageous in reducing early autumn frost damage. The factors most likely to limit growth potential in New Zealand are:

1) Lower temperatures in the growing season.
2) Out of season frosts.
3) Water deficits, especially during summer.
4) Low fertility sites or lack of fertilising.
5) Possible browse damage by opossums.

The climate model results agree with the findings from this study's experiments and furthermore, indicate specific locations. Again, however, the identified sites must also be assessed for the limiting factors given above (with the exception of low temperatures during the growing season) and this may further reduce potential sites.

CHAPTER I

INTRODUCTION

1. GENERAL

1.1 Species Description

Cunninghamia lanceolata (Lamb.) Hook. (Chinese fir) is an evergreen conifer in the Taxodiaceae (Redwood) family (Dallimore and Jackson, 1931; Den Ouden and Boom, 1982), occurring naturally in the sub-tropical region of central - southern China. *Cunninghamia* is a small genus comprised of two species (Welch, 1991); *C. lanceolata* and *C. konishii* or Luanta fir, a species very similar to *C. lanceolata* but having a smaller form and native to Taiwan province. *C. lanceolata* was first discovered (by western botanists) in 1701 or 1702 on Zhoushan Island, and introduced to Kew in 1804 (Dallimore and Jackson, 1931; Den Ouden and Boom, 1982). It has since been planted in Europe, Britain and the eastern United States as an ornamental species, and has been trialed elsewhere but does not appear to have been adopted on a large scale (see chapter XV). In China it has been cultivated as a timber species for over 1000 years (FAO, 1982; Hunan FRI, pers. comm.) and as such its silviculture is well developed. It is therefore difficult however to obtain an accurate picture of the natural distribution.

C. lanceolata is considered one of the most important trees in China, in terms of areas of planting, timber production and timber usage and has desirable features such as good form, fast growth and durable wood. It is widely distributed in central and southern China between 102 - 122 ^{o}E longitude and 22 - 34 ^{o}N latitude. It is planted in 16 out of the 21 provinces in China and constitutes over 50% of plantings in some provinces *e.g.* Fujian and Hubei (China, Tree Species Editorial Committee, 1978; Hunan FRI, pers. comm.; FAO, 1978; FAO, 1980). The best sites appear to be in the hilly and mountainous regions of the south eastern provinces *i.e.* Zhejiang, Fujian, Jiangxi, Hunan, Guizhou, Guangxi and Guangdong; so not surprisingly it is there that the greatest concentration of plantations is found (FAO, 1982). Figure 1.1 shows the provinces of China.

Altitudinal range varies according to region. In Hunan it is usually grown below 1200 m with the highest yielding forests between 300 - 600 m (Hunan FRI, pers. comm.). In the southeast most plantings occur below 240 - 300 m, while in the west the limit is up to

2000 m. In the northern areas *C. lanceolata* extends up to 1000 m in the north east and between 600 -1300 m in the north west (Cooperation Group of Chinese Fir, 1981b; FAO, 1982). With such a diverse range in climate, geography, and topography there is considerable provenance variation reported in the Chinese literature (see chapter III).

1. 2 Thesis Aim and Methodology

In late 1985 a group of New Zealand forestry people visited China, the visit (New Zealand Technical Forestry Mission to China) was designed to look at a wide range of forestry activities from forest management and research to forest products utilisation. Arising from this visit was an agreement between the Forest Research Institute (Ministry of Forestry, New Zealand) and the Chinese Academy of Forestry to organise a research exchange and cooperation programme. In 1987 the Forest Research Institute (FRI) received ten seedlots of *C. lanceolata* as part of this programme. Following this, a research contract, between the University of Canterbury and the Ministry of Forestry, was established. This study arose from the original research contract.

The species does not appear to have been planted (commercially) much outside China and Taiwan. In New Zealand it has been used mainly as a specimen tree in gardens and parks and occasionally in stands, however no detailed study of this species has been undertaken in this country. The aim of the research contract and this thesis then, is to provide, by way of literature review, and physiological and genetic experiments (of seedlings) on a variety of provenances, information on the prospects for growing *C. lanceolata* as a commercial forest tree species in New Zealand. The nature of the study, as dictated by the terms of the contract is necessarily broad, in order to accommodate the many aspects involved in assessing a tree species' potential in a new country.

While there is a vast amount of published literature on every aspect of *C. lanceolata* in Chinese (from China and Taiwan), there is only a small amount of literature in English on the species (mostly on specialised aspects). In order to provide useful information on the species' suitability for use as an exotic (*i.e.* outside its native range) this study aims to cover a wide range of environmental and physiological requirements for its growth, as well as an estimation of genetic variability in the provenance material used. This will provide a broad base of knowledge within the body of literature in English and, for the purposes of this study, will be used to give an indication of the physiological limitations to its growth.

In assessing a species' suitability to new regions, a variety of methods have been adopted. Wright (1962) summarised a suggested plan for testing exotics which briefly consisted of; climate matching, selection of species by desirable growth and wood properties (in their natural region), study of site preferences, small scale provenance trials with a selected range of provenances, and followed by large scale trials for stand

performance. Species introduction has formerly been hit or miss (Wright, 1962) and may or may not have included all or some of the above steps. In New Zealand, for example, early exotic species trials covered many species with different climate characteristics to that of New Zealand and provenance selection was not always studied until much later in the programmes (Shelbourne, 1986). Furthermore classical provenance testing usually involves lengthy field trials designed to measure growth over much of the species' rotation. In some South American countries exotics have been introduced primarily from climate matching (Golfari, 1963; see chapter XV). This method while usually successful, effectively excludes those species from different climates which may be able to adapt to the new climate.

In this study an alternative approach to assessing the suitability of *C. lanceolata* to New Zealand was adopted. A knowledge of physiological limitations to growth was used to determine where in New Zealand (if at all) would be suitable for *C. lanceolata*. Additionally, recently developed computer models were used to identify potential sites by climate matching. The study thus comprised the following components:

1. An overview of *C. lanceolata* management in China, and review of genetic research of *C. lanceolata*.
2. Studies of genetic variation in the study provenances by isozyme analysis and a nursery trial.
3. A range of physiological experiments to indicate how the species responds to environmental change.
4. Studies of growth pattern and dormancy requirements.
5. Investigation of wood properties of existing stands in New Zealand.
6. A study of palatability to opossums.
7. A review of *C. lanceolata* as an exotic plantation species and the use of climate modelling to predict suitable areas for its introduction.

2. TERMINOLOGY AND CONVENTIONS USED

2.1 Provenance Details

Seedlots of ten provenances were initially available, but one seedlot was found to be inviable. A further two seedlots, representing two different strains from the same stand, were added shortly after the commencement of the study. A total of eleven seedlots was used in this study; these represent a good range of latitude and altitude from its planted range in China. Unfortunately there was a lack of representation from the more central areas and the western and southern extremes. There is also a lack of collection details for the provenances; correspondence failed to elucidate the nature of the collections (*i.e.* number of trees seed collected from; year(s) of collection; stand details -

improved/unimproved trees, plus trees, open pollinated). The assumption was made that all seedlots were representative of provenances from those areas (open pollinated, unimproved stands) and collections were from the same year.

Provenance details are summarised in appendices A and B (climate, location and map). For ease of use provenances were numbered, reference to a specific provenance is given in this thesis by the prefix PV (provenance) followed by its number (1 - 12).

2.2 Statistical Analysis

For the majority of experiments where statistical analysis was required, analysis was carried out using the package SAS, Version 6 for PC's (SAS Institute Inc., USA, 1985). Where SAS was used the appropriate statistical procedure is stated for each experiment (*e.g.* general linear model for unbalanced designs, analysis of variance for balanced designs, regression *etc.*). Where SAS was not used, this is indicated. Unless otherwise stated, in analysis of variance (and forms of ANOVA) where statistical significance was found between treatments, separation of means was calculated using the Duncan multiple range t-test at the 95 % probability level.

In some cases specialised programmes were used (isozyme analysis, chapter III; wood properties, chapter XIII) and these are described in the appropriate chapter.

2.3 Reference Conventions

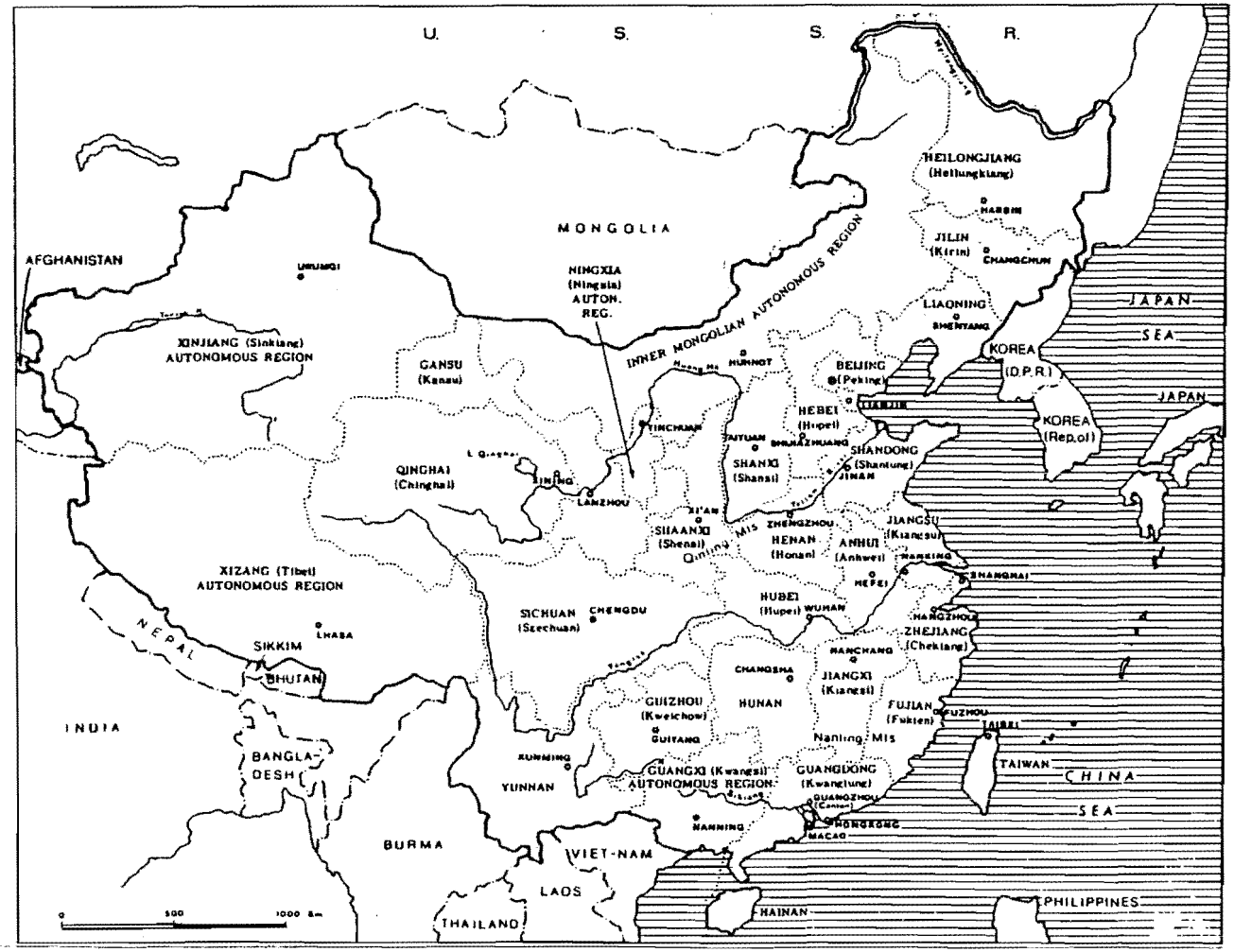
Species: Scientific names are used for all tree species to avoid confusion, especially amongst the less well known Chinese species. A list of corresponding common names of tree species referred to in this thesis is given in appendix C. Abbreviation of generic names to the first letter of that genus is used where the genus has been clearly used previously. The abbreviated form (*C. lanceolata*) of *Cunninghamia lanceolata* (Lamb.) Hook. is used throughout the thesis, as is that of *Pinus radiata* D. Don (*P. radiata*), the next most commonly referred to tree species.

China/Taiwan: While China and Taiwan are politically distinct entities they are considered in this study as one country in terms of *C. lanceolata* distribution and research. Thus Taiwan plantations of *C. lanceolata* are not considered as exotic plantings, although the distinction between Chinese and Taiwanese literature is made where appropriate.

Variables: Variables are often abbreviated for convenience in many of the experiments. Full definitions are given in the appropriate sections; however, a quick reference (to enable ease of reading) for most of the variables used is provided in appendix I.

References: A large number of these are non-English; the majority being Chinese, and the remainder in a number of languages (*e.g.* Portuguese, Spanish, Russian). Where there is no English summary, the foreign language is specified at the end, otherwise the English summary is specified. Where there is no indication of language the reference is in English. A large number of non-English references were however fully or partially translated (mostly by visiting Chinese scientists) and the author has an elementary knowledge of some Chinese and was therefore able to access some data. Thus while an English summary is specified for the reference many of these references were able to be used more extensively than the summary only. Conversely, other less important references (mostly used to support major references or used as background information) were not translated and the summary or abstract only was used.

Figure 1.1: Provincial Map of China



(From FAO, 1982)

CHAPTER II

AN OVERVIEW OF *Cunninghamia lanceolata*

As mentioned in Chapter I, the aim of this thesis is to assess the capability of *C. lanceolata* to grow in New Zealand, primarily by physiological and genetic means. The species has been managed for centuries and there is a vast body of knowledge with respect to its management. For prospective New Zealand growers there is also the need to have some indication of the management techniques that have been developed (mostly in China); this chapter aims to provide an overview of management aspects. Some findings in the literature may appear to conflict with others. While information may not necessarily be in conflict due to different experiments or conditions; it is difficult to elaborate given that the majority of the literature is in Chinese. As the literature is mainly in Chinese, with little communication possible with the authors, it is not possible to fully resolve conflicting findings.

1. PROPAGATION

A variety of methods have been studied and used to propagate *C. lanceolata.* The species is easily propagated by seed, sprouts (coppice), cuttings (Dallimore and Jackson, 1931). More recently tissue culture has been studied (Zhai *et al.*, 1984; Bigot and Engelmann, 1987).

1.1 Seed Germination

There have been a number of studies on germination. Standard procedure in Fujian is to soak seeds in water with a starting temperature of 40 ^{o}C, followed by shallow sowing, no stratification is carried out (Sweet, unpubl.). Germination was improved by treatment of 2 % solution of NH_4Cl at 40 ^{o}C for a short time (Fu *et al.*, 1988b). Soaking of seeds is best carried out for 20 - 24 hours, soaking for more than 24 hours is detrimental for germination (Ma and Liu, 1986).

It appears that while stratification does not increase the percentage of germinating seeds, it does however hasten germination by 2 - 4 days and gives more uniform seedling size. The germinating temperature used was 23 ^{o}C (Kung, 1976). While there was no significant difference in stratification at either 2 or 5 ^{o}C, a stratification time of between 2 and 6 weeks was optimal. Increased percentage of germination was also obtained by pre-soaking seeds in "magnetic" (presumably de-ionised) water for six hours; germination

was 80 % compared with 50 % for the untreated control (Wu, 1983). Further irrigation with "magnetic" water resulted in increased lateral root numbers and seedling heights compared with irrigation using normal water.

Storage of seeds does not seem to have been studied in depth. It is possible that seed stocks are not stored for a great length of time as there are seed shortages for planting programmes in some provinces, and seed transfer from provinces with surplus stocks may be necessary (China, Forestry Sector Loan Project, 1989a). Two studies on storage have contrasting findings. Yang (1964) found that optimum moisture content of seeds for storage was 14 - 18 % (from a tested range of 6 - 22 %) and the optimum temperature was 0.5 ^{o}C. Conversely Shi (1985) determined the optimum moisture content to be 7 - 8 %. It is possible that temperatures close to freezing may be sufficient to prevent deterioration in the short term as is the case with many other tree species (Tanaka, 1984).

Seed vigour is variable and under strong genetic control (Ye *et al.*, 1981c), selfing was the main factor in determining the number of tannin-like containing seeds (and presumably a correspondingly lesser number of healthy seeds). Seed respiration during germination was not correlated with first year growth, this was probably due to the wide variation of first year growth between and within races (Chiang and Hwang, 1974); however there was a highly significant correlation between seed weight, and respiration and early growth (Chiang *et al.*, 1972). In another study seed and seedling weight were found to be related to ATP content and respiration (Fu *et al.*, 1988c). Other recent studies have found that seed vigour and vitality can be related to dehydrogenase and peroxidase activity and germination value can be used as an indicator of vitality (Fu *et al.*, 1984; 1988a). Methods for testing seed vigour, germination ability, vitality *etc.* have been developed and include seedling vigour on vertical plate germinators (Chen and Chen, 1988; 1990), X-ray contrast (Wang, 1976), and TTC solution (Zheng *et al.*, 1984).

1.2 Cuttings

While cuttings are considered easy to root, it appears that this method is not favoured due to plagiotropic growth. A proportion does produce orthotropic growth and further tip cuttings may be taken from the resulting orthotropic shoots (Sweet, unpubl.). This predisposition to plagiotropic growth is also noted in *in vitro* tissue culture (see section 1.4 below). The ease of rooting cuttings may, in part, be due to the presence of growth hormones and lack of inhibitors in the buds (see section 1.4 below; Wang and Cheng, 1982).

1.3 Coppicing

One of the features of *C. lanceolata* is its ability to coppice (produce shoots from the base of the trunk). This ability is rare among conifers; only two other species with this ability

are reported: *Sequoia sempervirens* and *Pinus rigida* (Bigot and Engelmann, 1987). The new stem form does however deteriorate with an increase in felling age of the stool (Shih, 1976; Wu and Tai, 1980); after 18 years the taper on the new shoot is more pronounced than on stems of seedling origins (Shih, 1976). Through careful selection of stump height and diameter, age, and felling season, coppicing can produce faster and cheaper regeneration than standard seedling plantings (Shih, 1968; 1974; 1976; 1986; Wu and Tai, 1980; Lin and Hu, 1984). In many cases re-stocking by coppicing is carried out; however seedling establishment appears to be the preferred method, possibly due to pronounced tapering with age. Where re-stocking with seedlings or thinnings are carried out, the stumps are removed for firewood (NZFS, 1985).

1.4 Tissue Culture

Tissue culture techniques for *C. lanceolata* have been studied by Zhai *et al.* (1984). There were small amounts of growth inhibitors and larger amounts of gibberellins and cytokinin activity in shoot tissue, which may account for the high sprouting vigour of the buds (Wang and Cheng, 1982). *In vitro* vegetative propagation of apical sections and stem pieces (without needles) of mature (>50 years), juvenile (six months), and seedling tissue have been studied for ease of propagation (Bigot and Engelmann, 1987). Propagation was easy but plants derived from mature clones were plagiotropic in growth, and those derived from the juvenile clone and seed were orthotropic. Plants derived from the juvenile clone were more vigorous than those from seed, but this may have been due to a superior genotype of the clone and the heterozygosity of the seed material (Bigot and Engelmann, 1987).

2. SILVICULTURE

C. lanceolata is grown for use in shelterbelts, afforestation of bare mountain watersheds, and four around plantings: It is most extensively used in quick-growing plantations (FAO, 1982). The silviculture of the species is well developed, as would be expected; *C. lanceolata* has been cultivated in China for over one thousand years (FAO, 1982). The earliest record of timber use was *ca.* 300 AD (Menzies, 1988). The earliest report of a large-scale plantation dates back to 843 AD, while *managed* plantations were possibly present by the late 12th century and definitely by the late 15th century (Menzies, 1988).

There is also mention of archeological evidence of the existence of large trees in Hunan some 2000 years ago (Samset, 1976). A study on the cultural history of *C. lanceolata* concluded that the species has been cultivated at least since the Ming dynasty (1368 -1644) and possibly since the Han dynasty (206 BC - 220 AD). Regeneration from suckers (coppicing) was practised in the Southern Song dynasty (1126 - 1260) and intercropping since the Ming dynasty (Huang and Lan, 1988). The distribution of the

species was mainly in Anhui and Jiangxi provinces before the Ming dynasty and in the more southern provinces of Fujian and Hunan afterwards (Huang and Lan, 1988). Cheap, extensive river transport systems meant that timber could be readily transported to markets, and this undoubtedly aided in the development of plantations (Menzies, 1988).

2.1 Establishment

Formerly, using shallow planting techniques, plantings had low rates of survival (FAO, 1978). More recently a large number of planting studies have been carried out over the years and at present survival rates of over 90% are claimed (Sweet, unpubl.). For site preparation the area is cleared of almost all debris; pits or holes, 60 cm x 60 cm are then dug to a depth of 40 cm. One year old seedlings (1/0) are then planted to two thirds of their height below the soil (FAO, 1978). Alternatively in some sites a 50 cm deep trench is dug instead of holes, this method is supposed to preserve soil moisture better and so is presumably used in drier areas (FAO, 1978). The effect of site preparation and seedling size has been studied in Taiwan (Ho, 1968): Survival was better on unburnt than on burnt plots, and survival and growth of one year old seedlings (1/0?) was better than that of two year transplants (1/1?).

After planting, intercropping between rows is often practised as an alternative to weeding (FAO, 1978; 1982; Kumar, 1987; Menzies, 1988). Crop species are sequentially replaced by more shade tolerant species as tree canopy closure occurs. Annual crops including maize, peanuts and soybeans are followed by perennial cash crops, such as tung oil and tea oil (FAO, 1982; Kumar, 1987; Menzies, 1988). In the second or third year shallow ploughing is done and followed up in the fourth or fifth year with deep ploughing to 0.5 m, in addition a ditch is dug between rows in which grass and legumes are buried to increase the soil organic content (FAO, 1978). Intercropping while reducing weed competition also benefits soil fertility and microbial activity. Interplanting of *Amomum villosum* resulted in increased numbers of microbes, enzyme activity and soil respiration; there was accelerated decomposition and accumulation of nutrient in the soil (Chang *et al.*, 1988). In this respect there is a similarity to the benefits of mixed tree stands that have been used (see section 2.5 below).

2.2 Stocking

A variety of stockings have been tried ranging from 900 - 6000 stems ha^{-1} (FAO, 1978; Ruan and Dou, 1981). The present favoured stocking in Zhejiang and Fujian is between 3000 - 3600 stems ha^{-1} (Hong *et al.*, 1985; Sweet, unpubl.), although lower stockings of 2000 - 2500 stems ha^{-1} (FAO, 1978; FAO, 1982) and 1800 stems ha^{-1} (Ruan and Dou, 1981) appear to produce better volume growth. Spacing depends on the site; wide spacing is used on good sites, sites with gentle slopes, or in valleys and lower slopes and grown for short rotations (of 15 - 20 years). Closer spacing is used for poor sites, steep

slopes, or upper slopes; rotations are longer and early thinnings are used to allow development of larger logs (FAO, 1978).

Studies in Taiwan show that optimum stocking corresponds to stand density ratios of 80 - 120 %, the ratio is based on mean diameter and number of trees, basal area , or volume on a per ha basis (Liu, 1969). Initial stockings between 4400 - 2000 stems ha^{-1} were compared for a 20 year rotation, a stocking of 2500 stems ha^{-1} was considered best in terms of quality yield and revenue (Hung, 1969).

2.3 Tending

As has been mentioned, intercropping is used during early stages as an alternative to standard releasing. Releasing, where carried out, is done by hand; chemical sprays are generally not used. There is a need for intensive tending as young seedlings are not considered able to compete with weeds, especially in the first three years; early losses without proper tending can be 20 - 30 % and result in delayed canopy closure (China, Forestry Sector Loan Project, 1989b). In a trial using Velpar and Roundup, seedlings died after treatment with Roundup (although seedlings resprouted and commenced growth 40 - 60 days after treatment) and were less resistant to Velpar than pines (Kuo, 1984a). There is however, possible use for herbicide control. Root and shoot growth of seedlings in transplanting beds treated with 2, 4 - D and atrazine was better than those weeded by hand and there was no significant differences in survival between treatments (Kuo and Yao, 1971). Similarly chemical control of weeds at the nursery stage was 24 - 36 % cheaper than by manual weeding, although only 75 % of the weeds were eliminated (Zhou, 1989).

While intercropping can be of benefit, the intensive short rotations necessitate some form of additional fertilisation to avoid lower yields in successive rotations (FAO, 1982). Growth in second and third rotations was found to be 6.3 and 24.3 % less than in the first rotation at age 15 years (Fang, 1987). Pot trials of seedlings showed a typical growth response to N treatments (Fan and Yu, 1987). Field trials of Ca, Mg, and P greatly accelerated growth of 3 year old trees; shoot growth by as much as 80 % and dbh by 29 - 34 % (Li *et al.*, 1987). The application of P and K in yellow-red soils in China is necessary due to phosphate deficiencies, a 5 - 10 % volume gain is estimated (China, Forestry Sector Loan Project, 1989b).

Pruning is seldom practised, the species is purported to self prune (Hung, 1970). Pruning has little or no effect on height, diameter or basal area growth (Ch'en, 1968).

Canopy closure occurs at the 6^{th} or 7^{th} year and where appropriate, thinning to 50% intensity is done between 9 and 15 years (FAO, 1978). Thinning is seldom practiced in traditional plantations (FAO, 1982), although recent practises appear to favour thinning.

The extent of thinning of course depends on the initial and desired final stocking. In Fujian two thinnings are carried out (at ages 10 and 15 years), reducing the initial stocking from 3000 - 3600 stems ha^{-1} to 1200 - 1500 stems ha^{-1} (Sweet, unpubl.); conversely thinning is not considered necessary at lower stockings of 1800 stems ha^{-1} (Ruan and Dou, 1981). A single thinning is also used; removal of 20 - 30 % of the stand (initial stocking 3000 - 3600 stems ha^{-1}) is recommended by Hong *et al.* (1985). A single heavy thinning at age 14 years is also proposed for a 20 year rotation (Hung, 1969).

According to Hung (1970), rapid early growth of *C. lanceolata* requires early thinning by age 14 years and again at age 20 years, results showed that thinning was more profitable: Thinning, by itself or in conjunction with pruning, promotes significantly greater height, diameter, basal area and volume growth compared with unthinned (but pruned) stands (Ch'en, 1968). In another study the best final stocking following thinning to 2200, 3700, and 7200 stems ha^{-1} was 2200 stems ha^{-1} (Cai *et al.*, 1984). Thinning is also carried out according to site class; 1 - 3 thinnings may be required and final stocking is heavier on poorer sites compared with better sites (China, Forestry Sector Loan Project, 1989b).

2.4 Rotation Age

The rotation age varies according to site. Short rotations of 15 - 20 years are considered acceptable (FAO, 1982; NZFS, 1985) as there is a market for logs down to 5 cm diameter (FAO, 1982). Longer rotations of course produces larger logs; the rotation age varies between 20 - 40 years (FAO, 1982; Sweet, unpubl.). In most cases the intended end use is mainly for building materials, the focus is therefore on medium diameter timber (18 cm dbh), with a rotation of about 20 - 25 years (China, Forestry Sector Loan Project, 1989b). Taiwanese studies also indicate rotations of 20 - 25 years (Hung, 1969; 1970).

Intensive management can produce high yields and a rotation of 15 years in Hunan (Zhang *et al.*, 1988). In terms of biomass production in southern Jiangsu a rotation of 14 - 15 years is suggested (Ye and Jiang, 1982), while quantitative maturity (in biomass) at the Yangkou Forestry Farm, Fujian, occurs at 19 - 20 years (Ye *et al.*, 1984). For regeneration by coppice, short rotations of 10 - 20 years give adequate sprouting (Wu and Tai, 1980). The shorter rotations are most likely necessary to prevent excessive tapering at older ages while the regenerating sprouts are also more vigorous than seedlings.

2.5 Mixed Stands

While *C. lanceolata* is typically grown in large monoculture plantations, in natural forests the species appears to occur in mixed stands with deciduous (broadleaved?) species (Fong *et al.*, 1980). In terms of natural vegetation zones, *C. lanceolata* occurs in mixed

deciduous and evergreen broadleaved forests, and also in evergreen broadleaved forests (Richardson, 1966). Both of these forest types as well as modified secondary forests contain a large number of genera and species as canopy trees: It would therefore appear that *C. lanceolata* is, ecologically, not a monocultural species. In Anji county, Zhejiang province much of the bamboo forest was once mixed forest with *C. lanceolata* and *Pinus massoniana* (NZFS, 1985). Similarly Menzies (1988) reports that it is rare to find *Cunninghamia* occurring naturally in pure stands. Mixed plantings have been suggested by FAO (1978; 1982) primarily as a protection measure from pests and diseases rather than with respect to its ecology. Mixed plantings with broadleaved species are also recommended as protection against ice damage (Ouyang, 1987) and the advantages of mixtures with *C. lanceolata* have been discussed by Jiang *et al.* (1988). Species reported in mixed stands with *C. lanceolata* include: *Pinus massoniana, Sassafras tsumu, Michelia macclurei* or homana, *Paulownia tomentosa*, and *Robinia pseudoacacia. C. lanceolata* has also been planted as understory in *Araucaria angustifolia* stands in Brazil (Guidoni and Konecsni, 1982).

Where mixed plantings have been studied benefits have been apparent. In stands with *Pinus massoniana* overall soil microbial density was greater than in pure stands of either species (Zhang *et al.*, 1984); growth of anaerobic N-fixing and ammonifying bacteria was promoted as well as cellulose-decomposing fungi (Huang *et al.*, 1985). Land which is dry, infertile and considered unsuitable for *C. lanceolata* can be used by planting mixed stands of *C. lanceolata* and *P. massoniana* (China, Mixed Forest Study Group, Fujian, 1979). Nutrient cycling is increased in mixed stands with *Michelia macclurei* (Chen *et al.*, 1988), and association with this species does not appear to result in increased competition for nutrients (Liu and Zeng, 1990). Evidence of reduction in numbers of tortricids and termite pests of *C. lanceolata* (compared to pure stands) was also found (Yang *et al.*, 1987). Annual rates of decomposition and water retention capacity of litter was greater under broadleaved species (*Schima wallichii* and *Erythrophleum fordii*) than under either *C. lanceolata* or *P. massoniana* and therefore mixed stands of broadleaved and coniferous species was considered desirable (Wu *et al.*, 1990).

Losses in *C. lanceolata* to disease and insects decreased when mixed with *Sassafras tsumu*, and as with other species soil improvement was also apparent; soil organic matter was increased. Relative humidity was 6% higher and timber yields were 15 - 17 % higher and of better quality (China, Cooperative Research Group on Southern Mixed Stands, 1987). Increased growing stock was reported in 5 year old *C. lanceolata* when planted with *Sassafras tsumu* (Du *et al.*, 1988). Mixing was successful due to such factors as similar climate requirements and fast growth, different root systems (reducing nutrient competition), and different light requirements (China, Coordinating Group for Study of Mixed Stands in South China, 1987). *Paulownia tomentosa* also influenced microclimate conditions; direct solar radiation was intercepted by *Paulownia* crowns, and

wind force was reduced. Conditions of weak sunlight, high humidity and low evaporation rates were beneficial for growth of *C. lanceolata* and as a result photosynthesis, nutrient content and growth were all greater than in pure stands (Ni *et al.*, 1983).

3. GROWTH AND YIELD

3.1 Factors Affecting Growth

As mentioned in chapter I, the distribution of *C. lanceolata* is wide in terms of planted (geographic) range and altitude. Within this range there is some variation in climate, it therefore is of no surprise to find that growth and yield of *C. lanceolata* plantations also vary.

There are large climate differences associated with altitude. Below the altitudinal limit, growth rates do vary with altitude and/or site; site differences such as soil nutrient status, soil type, and drainage may also affect growth however. In general productivity is best in valleys of mountainous areas (FAO, 1982; China, Cooperative Group of Chinese fir, 1981a), decreasing in shaded slopes, sunny slopes, and ridges (Cooperative Group of Chinese fir, 1981a). Mountainous areas are more productive than hill and hilly lowland areas (China, Cooperative Group of Chinese fir, 1981a, Zhang *et al.*, 1980).

At the stand level, growth is correlated with temperature, precipitation (Yu, 1964; Cai *et al,* 1984), and relative humidity (Cai *et al.*, 1984). Most rapid growth occurs when mean monthly temperature is 22 ^{o}C and mean monthly rainfall is 200 mm (Yu, 1964). Adequate temperature and precipitation during the growing season are the primary factors for fast growth; deep, loose soil and adequate soil fertility are of secondary importance (Yang *et al.*, 1981). Best growth is found on deep, well drained soil with a pH of 4.5 - 6.5, in shaded valleys and lower slopes (FAO, 1982). In terms of phytogeographical zones based on natural vegetation *Cunninghamia* occurs within mixed deciduous and evergreen broadleaf forest, and evergreen broadleaf forest (Fong *et al.*, 1980; Zhang *et al.*, 1980; FAO, 1982). Soils are typically red, yellow, yellow-brown, and yellow-red earths (Zhang *et al.*, 1980; China, Cooperative Group of Chinese fir, 1981b).

Growth is sensitive to shortage of rainfall when temperatures are high, this has been demonstrated for 3 year old seedlings during peak growing times in July when low rainfall had an adverse effect on growth (Yu, 1964). Growth is not affected by (soil) salt concentrations of < 0.05 % but is reduced when concentration reaches 0.1 % (Cai *et al.*, 1984). Aspect has been shown to affect growth in Taiwan; growth increment was greater in east facing compared with west facing stands of young (up to 10 years old) trees (Chiao, 1968). Tree growth was correlated with humus content (in the 0 - 50 cm layer)

which was also positively correlated with root development (Li, *et al.*, 1981). The level of nitrate reductase activity (NRA) was higher in fast growing trees than those which were slower growing, it is possible that NRA could be used as an indicator of growth rate (Zhou *et al.*, 1985).

Growth rates can be improved by intensive management; high yields were obtained at 15 years by using deep planting, first grade seedlings, fertiliser and correctly timed thinning in Hunan (Zhang *et al.*, 1988). These same factors were also responsible for fast growth in young (2 year old) stands in Zhejiang (Liu and Wei, 1985) and in middle-aged stands also in Zhejiang (Wang *et al.*, 1986).

3.2 Growth Phases

Growth is most rapid between the 4^{th} and 11^{th} year and from June to September (Cai *et al.*, 1984). In terms of biomass production fastest growth between 2 - 18 years was in the 3^{rd} - 4^{th} year, and decreased in the 12^{th} - 13^{th} and 14^{th} - 17^{th} years (Ye and Jiang, 1982). In Taiwan a similar pattern is seen with dbh growth slowing down after 15 years and almost stopped by 20 years. Height growth also slowed considerably after 20 years, and maximum MAI (per stem volume) occurred between 24 - 32 years (Liu, 1982). Early selection of fast growing trees is possible (Liang, 1984), height growth at an early age (10 years old) was closely correlated with height at age 20 years (Spearman's rank correlation coefficient of 0.86) and less so at age 30 years (coefficient of 0. 57). Volume growth was closely related to height and when height was used for selection, maximum selection efficiency was obtained.

Seasonal growth occurs over a large part of the year, as much as 338 days in some areas (Wu, 1984). In general the growing season commences in April or early May and finishes in late September to November (Yu, 1964; Wei, 1981; Cai *et al.*, 1984). More detailed descriptions of shoot growth pattern and growing season are given in chapter XII (see also appendix A for growing season).

3.3 Growth Models and Yield Tables

A number of different growth models have been developed in the last ten years. Stem analysis equations have been examined; taper and volume ratio equations developed by Meng (1982) were considered more effective than previous equations. Height estimation using vertical section stem analysis was accurate for *C. lanceolata* (He, 1988).

The relationship between mean diameter and stand density has been studied, mean diameter was found to be inversely related to density but remained relatively invariant over different site conditions (Liu, 1984). A density control diagram has been developed for *C. lanceolata* which incorporated height and dbh curves for "full" density and natural and planned thinnings (Liu and Tong, 1980). The diagram was used for stands

established from either seedlings or cuttings, it can be used for planning and growth prediction and was accurate to more than 90 %. Optimum stand density tables for Zhejiang have been developed which account for crown overlap, and thus reduces error in calculating optimum stand density when dbh growth peaks (Xu, 1985).

Bertalanffy's model was considered suitable for describing volume growth in Taiwan (Feng and Yang, 1988). In Zhejiang, Tasiti Suzuki's forest transition matrix model theory was used to establish growth and yield models (Guo and Yan, 1985). Linear programming was then used to develop an optimum management regime.

A comprehensive study was made by Liu (1982) for seven plantations, regression equations for each plantation were formulated for age versus dbh, height, stem volume, CAI, MAI, form factor and growth rate. Regressions closely fitted the data (r^2 values 0.918 - 0.949, 0.894 - 0.980, 0.768 - 0.928, and 0.938 - 0.977 for dbh, height, stem volume and growth rate respectively). The regressions were all curvilinear of the form:

$$Y = a + bA + cA^2 + dA^3$$

where Y = variable (*e.g.* dbh, height)
a, b, c, d = coefficients
A = age (years)

Height, volume and diameter growth curves have been formulated for mountainous, hill and lowland (hilly) areas in Jiangxi, and have very high (0.974 - 0.995) r^2 values (Zhang *et al.*, 1980). Height curves are based on soil site index tables and the regressions used to derive the tables also fit the data extremely well (r^2 values 0.996 - 0.998), the regressions take the general form:

$$\text{Log } H = \text{Log SI} - x(1/A - 1/20)$$

where H = height (m)
SI = site index (H at age 20)
x = area coefficient
A = age (years)

Soil site indices have been used to classify planting areas in other provinces; Hunan, Guangxi, Yunnan, Henan, Guizhou, Guangxi (China, Cooperation Group of Chinese Fir, 1981a; 1983). Three series of site index curves have been developed from three recognised height growth patterns and site index tables have been constructed for 18 different areas (China, Cooperation Group of Chinese Fir, 1982).

3.4 Growth and Yield Data

Height growth is the most useful indicator of site and climate variation. Volume depends on both height and diameter growth and diameter growth is in turn related to stocking. As mentioned above site indices have been used extensively, the site index refers to the predominant mean top height of a stand (in metres) at age 20 years. While

this is useful for comparing growth at that particular age polymorphism may make such comparisons difficult at other ages. This has been alluded to in the above section where three different height growth patterns were found (China, Cooperation Group of Chinese Fir, 1982). Site indices are given in Table 2.1, in all cases valley sites are more productive compared with ridge or slope sites. Mountain sites are more productive compared with hill and lowland (hilly) sites.

There is a large amount of growth data of *C. lanceolata* in the literature, but for the purposes of this overview, comparisons are largely restricted to age 20 years. Sample height data are given in Table 2.2, data from trials in other countries, and comparisons with Chinese data of similar age are also given, where available.

The growth variation between regions can be attributed both to temperature and length of growing season. Length of growing season increases with decreasing latitude (China, Cooperative Group of Chinese fir, 1981b; Wu, 1984) and is thus related to winter and annual temperature. The Fujian provenances are located on the southeastern coast and experience warmer temperatures than more interior provenances at similar latitudes. Guangdong provenances while having a longer growing season show much poorer growth; at these latitudes it is likely that temperatures are above optimum levels.

Volume yields and productivity are dependent upon site, climate and stocking. However sites favouring height growth are similarly highly productive in terms of volume growth. Generally a standing volume of 250 - 350 m^3 ha^{-1} after 20 years is considered good (FAO, 1982) although high yield areas can yield up to 400 m^3 ha^{-1} (FRI, Hunan, pers. comm.).

Productivity as mean annual increment (MAI) of volume is shown for various sites in Table 2.3. Standing volume (derived from MAI*age) varies at age 20 from less than 120 m^3 ha^{-1} in the southern zone, to over 420 m^3 ha^{-1} in the central zone (China, Cooperative Group of Chinese fir, 1981b). Some exceptional sites are included to indicate the species' potential. Guizhou Jinping is considered as one of the best production areas and at age 18 years had a standing volume of 736 m^3 ha^{-1}; Xihou forest in Fujian Nanping has very high growth and at age 39 had 1170 m^3 ha^{-1} (China, Cooperative Group of Chinese fir, 1981b). This same stand was measured again at age 64 years and had 1185 m^3 ha^{-1} (MAI of 18.7), indicating that volume growth had slowed considerably (Lin *et al.*, 1984).

4. PESTS AND DISEASES

In China there appears to be no major (economic) pests or diseases (FAO, 1978; 1982), presumably due to a long history of co-evolution within its natural distribution. Although this is claimed, a large number of cases have been reported in the literature in recent years. Quite often these are localised outbreaks and the degree of economic importance may be hard to assess, nevertheless a brief description of these cases is given as an indication of likely problems and possible control measures.

4.1 Animal

On the mainland there is very little reported animal damage; squirrel being the only reported case (Zhu, 1988). Bark damage from squirrels is more documented in Taiwan (Kuo, 1984b; Kuo *et al.*, 1984; Lin and Kuo, 1987) and this is mentioned in chapter XIV. Damage resulted in reduced volume, height and diameter growth (Kuo, 1984b), and was most severe in pure stands with high stocking (Kuo *et al.*, 1984). Utilisation of damaged trees was 55% compared to 70% for healthy trees (Kuo, 1984b). Both *C. lanceolata* and *Cryptomeria japonica* appear to be preferred over other conifer species (Kuo, 1984; Chien *et al.*, 1988) and although damage was greater for *C. lanceolata,* growth was less affected (Kuo, 1984b). In China preferential browsing (bark stripping) was also seen on *C. lanceolata, Pinus massoniana, Cryptomeria fortunei* and a few broadleaf species (Zhu, 1988), although it appears that *P. massoniana* was the preferred species.

There is a relationship between squirrel damage and chemical composition of the wood with high sugar content correlating with high bark damage (Kuo *et al.*, 1982). The presence of an allele of peroxidase has been suggested as causing trees to convert phenolic compounds in the bark to bitter tasting quinones thus reducing damage compared to trees not possessing the allele (Huang *et al.*, 1982). Further work on the relationship of bark resin content and squirrel damage has been carried out by Hwang *et al.* (1984) with the object of breeding squirrel resistant strains. Poisoning is an effective method of control using klerat (brodifacoum) in baits (Chien *et al.*, 1988; Kuo and Liu, 1988).

Other browsing pests are not found in China, but possum, rat, and wallaby damage have been reported in Australia (see chapter XIV).

4.2 Insect

A number of insect pests have been recorded, with possibly the most serious being a tortricid, *Polychrosis cunninghamiacola.* It has only recently been discovered in Taiwan since 1985 (Chang and Sun, 1987), and appeared to be specific to *C. lanceolata.* Damage

reached up to 30% of shoots so it is likely that the species has the potential to severely affect plantings. *P. cunninghamiacola* is an important pest in China (FAO, 1982) but control in the form of strains of *Bacillus thuringiensis* has been developed and in tests, mortality of *P. cunninghamiacola* was 90.9% (Liu and Tan, 1984). Cultural practices such as mixed stands have also been found to reduce attacks (Yang *et al.*, 1987).

Termite damage has been recorded but *C. lanceolata* is considered to be moderately resistant to termite (Lenz and Dai, 1985). Cones of *C. lanceolata* are however susceptible to *Macrotermes barneyi* and *Odontotermes formosanus* (Wang, 1984), and *Cryptotermes declivis* damaged old beams and furniture of *C. lanceolata* (Zhu, 1982). Again mixed stands reduce attacks from *M. barneyi* (Yang *et al.*, 1987), and the natural resistance to *Reticulitermes chinensis* is due to cedrol and other minor components of extractives in the wood (Lu *et al.*, 1987).

A bark beetle, *Phloeosinus spp.* is considered an important pest in many provinces although there appears to be natural biological control from *Dinotiscus* sp. parasitizing the larva of *P. perlatus* and the adults being attacked by the pathogen *Beauveria bassina* (Zhao and Cao, 1987). However parasitism of *P. sinensis* from the *Eurytomidae* and the *Ichneumonidae* is low, around 18 % (Su and Zhou, 1988). Effective control with insecticides has been achieved with any of 80 % DDVP (dichlorus) and 25 chlordimeform, 80 % DDVP, 50 % fenitrothion, or 75 % phoxium (Su and Zhou, 1988; Zhao and Cao, 1987; Zhao *et al.*, 1988). A pyralid, *Euzophera batangensis,* destroys stem cambium. Control by application of 40 % dimethoate is recommended (Wang and Wang, 1988).

A new pest, *Dichomeris* sp., was reported by Qian *et al.* (1990). This insect damages cones and is distributed in five provinces. Another beetle pest is the cerambycid *Semanotus spp.*, biological control from ectoparisitic wasps appears to be very effective. Control of *S. sinoauster* by *Ontsira palliatus* was about 90 % (Zhang *et al.*, 1987) and rate of parasitization by *Scleroderma* on *S. bifasciatus* was 70 % (China, Forest Research Institute, Guangdong Province, 1980). Parasitism of another cerambycid, *Ceresium sinicum*, by another wasp, *Paracerchysius ceresii*, has been reported by Liao and Tachikawa (1984). Thus while there are many potential pests it is probable that effective natural biological control reduces their impact under normal situations; chemical insecticides are also effective in the absence of adequate biological control.

4.3 Pathogen

There are many reported cases of diseases caused by pathogens, the most widely reported being anthracnose. The disease can cause severe damage to young plantings by attacking previous season's needles, spreading through shoots, necrosis of needle tips in older branches (Li, 1980). The causal agent is *Colletotrichum* sp. (Li, 1980; Zeng *et al.*, 1981)

although latent infection of *Glomerella cingulata* also produces the disease (Chuandao *et al.*, 1980; Den, 1988). Anthracnose affects weak trees more readily (Zeng *et al.*, 1981), and chlorotic needles were predisposed to infection (Li, 1980; South China Forest-Plant Quarantine Service, MFPRC, 1980). Unfavourable site conditions causing light deficiency favours development of infection; the disease is not considered significant where *C. lanceolata* is endemic (South China Forest-Plant Quarantine Service, MFPRC, 1908). The severity of the disease is not correlated with latent infection rate (Den, 1988) as healthy trees showing no symptoms can still be infected (Zeng *et al.*, 1981). Increased enzyme activity (peroxidase and polyphenol oxidase) at the front of the infection is an indication of host resistance (Su and Tan, 1987).

Anthracnose develops rapidly when temperature is 20 - 25 ^{o}C, but rainfall and relative humidity seem to have little effect (South China Forest-Plant Quarantine Service, MFPRC, 1980). Infection disappears when average temperature falls below 10 ^{o}C apparently when reducing sugar content is high (Den, 1988). Control is largely silvicultural, presumably to alleviate site conditions, and fungicides are applied during time of infection (Zeng *et al.*, 1981). Recently a study on biological control has indicated that the bacterial product PRS5 of *Bacillus subtilis* is antagonistic to anthracnose (Yang, 1990a).

Other diseases affecting leaf and shoot tissue are needle, twig, terminal bud blights and shoot dieback. Needle blight has several causal agents: The fungus *Bifusella cunninghamiicola* has been recorded on *C. lanceolata* in Okinawa, Japan (Ogimi and Korf, 1972) and subsequently at Chiba near Tokyo, (Saho and Zinno, 1972), it has been renamed *Soleella cunninghamiicola* (Saho and Zinno 1975). Two other fungi associated with needle blight were collected in Tokyo, *Bartalini cunninghamiicola* and *Discosia pini*, although only *Bartalini cunninghamiicola* was considered pathogenic (Kobayashi and Zhao, 1987). A bacterial pathogen, *Pseudomonas cunninghamiae,* caused needle blight in Jiangxi, invading through stomata and wounds (Anon, 1977).

Twig blight caused by *Botryosphaeria cunninghamiae,* was reported in Fujian, (Huang, 1977). Terminal bud blight was caused by *Phomopsis* sp., although the incidence was related to aspect and site; effective control with fungicides iron metharsenate and monox was possible (Su *et al.*, 1981). The fungus *Pestalotia apiculata* caused shoot dieback affecting seedlings and young trees (Huang, 1983). Damping-off, a fungal disease affecting nursery seedlings and young trees was effectively controlled by "Terrazol" and "Vapam" (Young and Wang, 1976), "Vapam" was effective for seedlings and up to three year-old trees (Wang, 1968). Biological control has also been successful using *Gliocladium virens* strain F051 which has an antagonistic effect on the causal agent of damping off, inhibiting hyphal growth (Lin *et al.*, 1988). Another form of biological control is found in the strain PRS5 of *Bacillus subtilis* which is antagonistic to 10

pathogenic fungi including *Rhizoctonia solani* (damping-off) and *Colletotricum gloeosporoioides* (anthracnose), the strain strongly inhibited *R. solani* (Yang, 1990a). Cultures of the strain used to treat nursery soil achieved up to 87 % control (Yang, 1990b).

The root knot nematode, *Melioidogyne incognita*, has been found in nurseries in Taiwan, but this appears to be a minor occurrence (Wang, 1972). Root rot (*Pythium ultimum*) has been recorded in Sichuan (Qiu *et al.*, 1986). In Tokyo *C. lanceolata* was resistant to white root rot (caused by *Rosellinia necatrix*) following serious outbreaks from 1976 - 1979, shade tolerance of *C. lanceolata* was thought to account for its resistance (Ito and Nakamura, 1984). Wood rot seems to be less of a problem due to the presence of extractives which inhibit mycelial growth of fungi (Lu *et al.*, 1987; Shieh *et al.*, 1986; Shieh *et al.*, 1987; Wang *et al.*, 1989).

Table 2.1: Site Indices (SI) for *C. lanceolata* in Various Provinces and Sites

Site	HE	GD	YN	GZ	JX	GX
Mtn Ridge/Top	6-8	10-14		12	12	14
Mtn Slope	10-12	16-18		16-18	14-18	17
Sunny	8-10[i]					
Shaded	12-16[i]					
Mtn Valley	12-16	20-22	14-20[i]	20-22	16-18	20
Hill Ridge	6-10	8-10				
Hill Slope	8-10					
Sunny		10	12-16[ii]			
Shaded		12-14	14-20[ii]			
Hill Valley	12-14	14-16	18-22[ii]			
Lowland Top	10-12					
Lowland Slope	8-10					
Lowland Valley	10-12					

Notes: HE: Henan GD: Guangdong YN: Yunnan
GZ: Guizhou JX: Jiangxi GX: Guangxi
[i] Mountains > 1600 m [ii] Mountains < 1600 m

(from China, Cooperation Group of Chinese Fir, 1981a; 1983)

Table 2.2: Sample Heights (Ht) at Various Ages (A)

Site	Lat (°N)	Ht (m)	A (yr)	Source	
AUSTRALIA	17 - 27[i]	12.5-18.6	18-21	Nielsen, pers. comm.	
AH, Huoshan (I_2)	31 - 32	10.6	20	FAO, 1982	222*
AH, Qimen (II_{3b})	29 - 30	13.3	20	FAO, 1982	236*
HU, Huitong (II_2)	27 - 28	15.1-18.2	19	Yeh and Ch'en, 1964	
		14.9	20	FAO, 1982	
FJ, Jian'ou (II_{3c})	27	17.8	20	FAO, 1982	275*
FJ, Nanping	26° 50'	18.3-18.8	20	Lin *et al.*, 1984	
GZ, Jinping (II_2)	26 - 27	14.0	20	FAO, 1982	
		13.0-17.2	20	Yeh and Ch'en, 1964	
FJ, Pingnan (II_{3b})	26 - 27	16.2	20	FAO, 1982	275*
JX, Suichuan	26° 30'	9.0-14.0	20	Wu, 1984	
HU, Jianghua (II_{3c})	25	16.2	20	FAO, 1982	
GD, Yunan (III_a)	23 - 24	7.3	20	FAO, 1982	
GD, Xinyi (III_a)	22 - 23	8.0	20	FAO, 1982	338*
TW, various		12.9-17.1	20	Liu, 1982	
NEW ZEALAND	38[i]	12.2-14.3	25	Rotorua, this study	
TW, various		14.2-18.2	25	Liu, 1982	
FJ, Nanping	26° 50'	20.5-22.1	25	Lin *et al.*, 1984	
JAPAN, Chiba	35° 30'	11.7-15.7	29	Negisi, pers. comm.	
TW, various		14.4-18.3	29	Liu, 1982	
FJ, Nanping	26° 50'	22.2-24.7	30	Lin *et al.*, 1984	
JX, Suichuan	26° 30'	9.4-19.6	30	Wu, 1984	
NEW ZEALAND	39[i]	23.1	58	Camp Huinga, this study	
FJ, Nanping	26° 50'	26.2-30.2	60	Lin *et al.*, 1984	
Southern Sichuan		20	60	Anon., 1960	

Notes: AN: Anhui HU: Hunan FJ: Fujian
GD: Guangdong JX: Jiangxi TW: Taiwan
GZ: Guizhou
[i] Latitude is °S
* approximate growing season (days), from Wu, 1984.

Table 2.3: Productivity (MAI) at Various Ages (A)

Site	MAI*	A (yr)	Source
Type A (SI 20)	19.5	20	China, For. Sect. Loan Proj., 1989b
Type B (SI 18)	13.5	20	
Type C (SI 16)	10.5	20	
JX, Mountains	7.5-14.9	20	China, Coop. Grp. of Ch. Fir, 1983
GZ, Mountains (II_2)	12.1-21.3	20	
GZ, Jinping (II_2)	40.9	18	China, Coop. Grp. of Ch. Fir, 1981b
FJ, Nanping (II_{3c})	30	39	
Zone II_1 (2)	4.6-12.1	20	
Zone II_1 (3)	14.5	20	
Zone II_2	15.2	20	
Zone II_{3b}	>7.5	20	
Zone III_a	7.5	20	
Zone III_b	<6.0	20	

Notes: GZ: Guizhou JX: Jiangxi FJ: Fujian

* MAI = $m^3\ ha^{-1}\ ann^{-1}$

CHAPTER III

GENETIC RESEARCH OF *Cunninghamia lanceolata* IN CHINA: A LITERATURE REVIEW

1. INTRODUCTION

As a major tree species *C. lanceolata*'s silvicultural technology and knowledge is well researched given the long history of management (see chapter II). Genetic research has however only recently been extensively undertaken. Provenance testing of *C. lanceolata* has been in operation since the fifties although larger and better designed tests were initiated from 1977 onwards (Hong, 1987). Geographic variation is predominantly clinal and correlated with temperature and, in part, latitude. The first seed orchard, Yangkou Forest Farm in Fujian province, was established in the sixties. From 1972 more seed orchards, both seedling and clonal, have been started; these seed orchards supply up to 30 % of seed requirements for annual plantings. Progeny testing has also been carried out and from these improved first and second generation seed orchards have been established (Hong, 1987). It is estimated that 10 - 15 % gain (in productivity) can be made through tree breeding and improvement (China, Forestry Sector Loan Project, 1989b).

In this literature review genetic aspects of *C. lanceolata* research will be covered in order to provide some background information necessary for a New Zealand forester considering the introduction of *C. lanceolata.* Other aspects of *C. lanceolata* research relevant to the study are included in the appropriate chapters. A short introduction to climate and geographic distribution is included in the review however, as these are important factors in any study of genetic variation and tree improvement.

2. CLIMATE

China's climate pattern is controlled by three features: Monsoons, mountain ranges and cyclones (Hsieh, 1973). Wind direction is strongly seasonal; in the winter monsoon the winds in central China are usually from the north and northeast, while in the summer monsoon southeast winds predominate. Since winds from the continent are dry and cold and those from the ocean are moist and warm, rainfall is also seasonal and reaches its maximum in summer and minimum in winter (Hsieh, 1973). Mountain ranges also affect the climate, the east-west alignment of both the Qinling ranges to the north (*ca.* 34 ^{o}N)

and the Nanling ranges to the south (25 °N) closely correspond to the north-south distribution of *C. lanceolata* (see chapter I). Both ranges delay and reduce the effects of cold fronts (originating from Mongolia) during winter (Watts, 1969), and act as barriers to the northwards flow of rain-bearing winds during the summer (Hsieh, 1973). As a result there are distinct climatic boundaries that are closely related to agricultural patterns of cultivation (Hsieh, 1973). Figure 3.1 shows the major topographical features of China. Extratropical cyclones tend to cause abrupt weather changes, and occur most often in spring followed by winter, autumn and summer (Hsieh, 1973). More damaging are the tropical cyclones originating in the western Pacific. These storms are most prevalent during July to September (Watts, 1969; Hsieh, 1973) and are particularly important along the coastline both in terms of damage and rainfall; however intensity and frequency of tropical cyclones diminish as they pass over land (Watts, 1969).

Generally *C. lanceolata* prefers warm, moist environments, with a mean annual temperature of 15 - 23 °C and mean annual rainfall of 800 - 2000 mm, the January mean temperature is 1 - 12 °C (FAO, 1982; Hunan Forest Research Institute, pers. comm.). In high yield areas mean annual temperature is 16 - 19 °C, mean annual rainfall is above 1200 mm, relative humidity 80 % and there are 300 or more days with temperature above 5 °C.

2.1 Rainfall

Rainfall variation in areas of plantings is seasonal; it is characterised by a pronounced summer monsoon maximum and a comparatively dry winter (Watts, 1969). Over 80 % of the annual rainfall occurs between May and October (Hsieh, 1973). The maximum is most often in June, but in outlying areas, away from the Yangtze (Chang Jiang) and southeastern provinces, maxima occur in July or August. Annual rainfall is greatest in the southeastern provinces (>2000 mm) and decreases towards the northwest (Watts, 1969). This as mentioned above, is due to the presence of mountain ranges acting as physical barriers (Hsieh, 1973). The northern limit of *C. lanceolata*'s distribution is close to the 750 mm isohyet which parallels the Qinling ranges and the Yellow river (Huang He), while the 1100 mm isohyet (which is just below the high yield range of 1200 + mm) lies roughly along the Yangtze (Watts, 1969; Hsieh, 1973). Rainfall, and particularly the amount of summer (growing season) rainfall appears to be limiting in these areas. Rainfall distributions are given in Figure 3.2, and seasonal patterns for sample sites are shown in Figures 3.3 and 3.4.

2.2 Temperature

Temperature is similarly seasonal. January is the coldest month in all areas, with mean temperatures ranging from 1 - 2 °C in the northern zones to 12 - 15 °C in the southern zones (China, Cooperative Group of Chinese fir, 1981b; Wu, 1984). Frosts occur, but

are few to the south of the Yangtze where winter temperatures are 3 - 5 °C (Watts, 1969). Thus there is a clear trend of colder (winter) temperatures with increasing latitude, although altitude also affects winter temperatures. Mean January isotherms are shown in Figure 3.5. Mean January temperatures are below freezing for high altitude (960+ m) sites in the central zone (-3.4 to -0.4 °C) and are up to 7 °C colder than lower altitude sites in the same areas (Wu, 1984). These high altitude sites are generally considered unsuitable for planting. Absolute minimum temperatures also follow the north-south trend ranging from 0.5 °C in the south zone to -20.9 °C in the north (Wu, 1984), -24 °C has also been reported in the north (China, Cooperative Group of Chinese fir, 1981b).

Mean monthly temperature throughout the area is hottest in July, but there is no clear trend in terms of latitude as is the case with January temperatures. In most areas temperature is between 25 - 30 °C, but towards the western most parts and in high altitude sites this drops to 19 - 25 °C (Wu, 1984). Mean annual temperatures do show a general north-south trend similar to that of mean January temperatures and is probably a result of the winter temperature pattern. In the northern zone the range is 14 - 16 °C, while the southern zone is 19 - 23 °C (Wu, 1984; China, Cooperative Group of Chinese fir, 1981b). High altitude sites are 5 - 8 °C colder (Wu, 1984). Figure 3.6 shows mean July isotherms and mean annual isotherms are shown in Figure 3.7.

Departures from mean annual, summer and winter temperature are very small (respectively 1, 0.4 - 1.8, 1.0 - 2.0 °C for one standard deviation; Watts, 1969)), indicating that temperature is relatively stable in it's seasonal pattern.

2.3 Other Climatic Factors

Relative Humidity: This follows the seasonal pattern of temperature and rainfall, but the differences are not as pronounced as these two factors. Mean humidities are generally over 75 % in winter for areas south of 35 °N, while south of the Yangtze humidity is usually greater than 80 % (Watts, 1969). A look at climate station data from Watts (1969) in fact suggests that humidity within *C. lanceolata*'s area of distribution is relatively uniform in most sites. Mean annual relative humidity ranges from 70 - 83 %, and those sites with slightly greater humidity are generally located in the central zones (II) of *C. lanceolata* production areas (see section 3.1 for classification).

Evapotranspiration: This is similarly seasonal and is greatest in summer. Annual potential evapotranspiration regions broadly correspond to mean annual isotherms, and the regions corresponding to *C. lanceolata*'s distribution all experience an average water surplus. Thornthwaite moisture indices show that these are all humid regions except for the Nanling ranges which are perhumid (Watts, 1969). This lack of water deficit (despite dry winters) appears to be an important climate factor for *C. lanceolata* as experience in

Brazil indicates that areas with water deficits are unsuitable for the species (Golfari, 1968; see chapter XV).

Snow and Frost: Over central China snow falls on average 10 days per year between the beginning of December and mid-March, and the frequency decreases sharply towards the south. There are fewer than 5 days of snow per year during January or February on the Zhejiang coast, while along 25 ^{o}N there is only one day per year around late January (Watts, 1969). The duration of snow cover is equally short (Figure 3.8).

Frost is a frequent occurrence in the North China Plain, but to the south of the Yangtze (where the majority of *C. lanceolata*'s plantings are sited) frosts are present but fewer (Watts, 1969). Mean number of days above 0 ^{o}C are shown in Figure 3.9; this is over 350 days for *C. lanceolata*'s range. Frosts do still occur, as evidenced by absolute minimum temperatures given in section 2.2 above.

3. GENETIC VARIABILITY

3.1 Geographic Distribution Studies

A number of studies have been carried in recent years. Some have concentrated on ecological and geographical aspects (*e.g.* Pan *et al.*, 1980; Sheng *et al.*, 1981; Cooperative Group of Chinese fir, 1981a & b). Others deal more with provenance testing *per se* (Chen *et al.*, 1980; China, National Collaborative Research Group on Provenance Trial of Chinese Fir, 1988; Guangdong Provenance Trial Cooperation of Chinese fir, 1986). Earlier work showed that 12 different forms of *C. lanceolata* (possibly varieties) were present in Hunan, Guizhou and Jiangsu (Yeh and Ch'en, 1964). One form (Kang sha, grey leaved with recurved cone scales) had greater height, diameter and volume growth, while a form with fragrant wood (Huang zhi sha) had high physical and mechanical properties.

With a wide geographical distribution, differing conditions of climate, topography and soils occur. Pan *et al.* (1983) studied the growth variation of 32 provenances at age two years by principle component analysis (PCA) of seven growth characteristics. Of these, total height growth, annual height growth and crown diameter accounted for 98 % of observed variation. The relationship between the growth characteristics and nine ecological factors were analysed by stepwise regression. Three ecological factors; latitude, average annual relative humidity, and average annual precipitation were found to be correlated with growth.

Sheng *et al.* (1981) also examined (seven) climate factors by PCA to predict growth. Six discontinuous groups were obtained and from these the geographical range of *C. lanceolata* can be divided into three zones and six regions:

Zone	Region
Northern (I)	Eastern (I_2), western (I_1)
Central (II)	Eastern (II_{3a}, II_{3b}, II_{3c}), middle (II_2), southwest (I_1)
Southern (III)	Southern (III_a, III_b)

Productivity varies between regions and zones reflecting different climates. Some growth data for each region are summarised (China, Cooperative Group of Chinese fir, 1981b) and the best production areas occur in the central zone regions. In particular locations around the Nanling mountain range are considered very good as well as other sites already mentioned above (Jinping, Huitong, Nanping-Xihou). The production zones and regions, along with the locations of the provenances used in this study are shown in appendix B.

More detailed site classification of *C. lanceolata* in southern provinces has been studied and has been described in chapter II, section 3.3 (Zhang *et al.*, 1980; China, Cooperative Group of Chinese fir, 1981a). Further work has integrated geographic regionalization and zoning with site classification to provide guide-lines for intensive cultivation by predicting productivity and use in site choice (China, Cooperative Group of Chinese fir, 1983).

In Taiwan studies have generally concentrated on comparisons with the endemic species *Cunninghamia konishii*. The two species are very similar morphologically; however growth of *C. lanceolata* appears to be inferior to that of *C. konishii,* at least at altitudes between 600 - 2000 m (Wang, 1978). Varieties of *C. lanceolata* (large-leaved and glaucous) were similar in growth but still inferior to *C. konishii* from the fourth year after planting to age 11; *C. konishii* was recommended for afforestation at altitudes of 700 - 2000 m (Liu, 1974). Growth differences were found among seedlings of 4 provenances of *C. lanceolata* grown under 3 light intensities (Chiang and Wang, 1982). While there was strong provenance x light interaction, best growth for all provenances occurred at 1000 foot candles.

Respiration rates of germinated seeds and seedling growth of seven different races of *Cunninghamia* were studied by Chiang *et al.* (1972) and Chiang and Hwang (1974). Significant differences between and within races for respiration; 30 - 35 % of the variation was between races (Chiang *et al.*, 1972). Significant differences were also found between races in one year seedlings for stem length, branch number, branch length, and leaf length, but not for diameter (Chiang and Hwang,1974). These differences were not apparent in the second year. There was no correlation between respiration rates of germinated seeds and growth. In one study some variation was found between seedlings grown from seed from 17 different stands and 7 areas; significant

differences between areas were seen in survival and timing of dormancy (Hwang and Sun, 1986).

While the above studies are more concerned with productivity of the species as a whole, the findings indicate a large amount of environment diversity within *C. lanceolata* 's geographic range (in China). In the absence of seed and pollen exchange, either through cultural practice or geographic discontinuity, it would be expected that genetic variability would arise between populations. However given the long history of management and the ease of transport between regions it is likely that some form of genetic mixing (such as seed exchange) has occurred (see chapter II). Provenance testing would provide some quantitative measure of genetic variability.

4.2 Provenance Testing

Classical provenance testing deals with actual tree growth of different provenances under similar conditions; Chinese studies of *C. lanceolata* have shown that strong provenance differences exist. Within the planted distribution of *C. lanceolata* (and indeed for most of the heavily populated areas of China), the existing vegetation has been modified by man over a long period (Richardson, 1966). While there are a large number of provenances, it is unclear as to whether these provenances are from natural populations or derived from years of intensive management where selection may have been carried out. It is likely that the latter is the case for the majority of provenances as within the planted distribution of *C. lanceolata* there is very little remaining natural forest (see Figure 3.10, FAO, 1982).

Chen *et al.* (1980) found significant differences in height growth, biomass and leaf index between eleven provenances after five years. There was a consistent pattern in height growth differences from ages two to five years, although differences in growth became less over time (apart from the worst performing provenance). Height growth was negatively correlated with latitude and longitude at the seedling stage, and negatively correlated with longitude only at age four years.

Rankings in biomass production also correlated with "natural" regions of *C. lanceolata.* Accordingly provenances were divided into three breeding zones; central, general, and border; with central zone provenances having the greatest biomass, followed by the general zone and then the border zone. The zones broadly correspond to those given above: The central zone is located around the Nanling - Fujian area (II_{3c}, II_{3b}), the general zone is to the north and south of the central zone, and the border zone is the periphery of the range of plantings. The central zone provenances were also more adaptable to a wide range of sites than those from the border zone.

Provenance differences were significant in two trials conducted in Guangdong province (Guangdong Prov. Trial Coop on Chinese fir, 1986). In the first trial twenty

provenances on three sites were analysed after nine years. On average the five best provenances had 210 - 254 % more volume production than those of the next five provenances and differences between the best and worst provenances were as much as 4 - 8 times. Differences were not as large but still significant in the second trial involving 56 provenances on five sites, grown for five years. This may have been due to shorter growth phases (186 - 201 days for the best provenances in the second trial compared to 210 - 238 for those in the first trial). Similar to the findings of Chen *et al.* (1980), heights from age 2 - 9 years except for age 8 years was significantly correlated with height at age 1 year; correlation coefficients ranged from 0.405 to 0.611. Coefficients increased with age *i.e.* Correlation coefficients of heights for age 2 with ages 3 - 9 years were 0.670 - 0.834 ; for age 3 with ages 4 - 9 years 0.867 - 0.772 (all highly significant).

Interestingly provenance x site interactions were not significant indicating that many provenances were adaptive to a wide range of sites. Good provenances identified were: Rongshui (Guangxi); Lechang (Guangdong); Jinping (Guizhou), Jian'ou (Fujian); and Quannan (Jiangxi). In particular, Rongshui and Lechang (these two provenances are represented in this study), performed well over the whole range of sites. In general, good provenances were centralised in the Nanling area and characterised by; a long growing season, low seed production, high resistance to pests and diseases, and a high degree of adaptability to different sites.

Poor provenances exhibited slow growth and a low resistance to pests and diseases, in at least one provenance (Sichuan Dechang); this was related to different climate conditions compared to its native climate. Zhejiang Longquan was also considered a poor provenance and is represented in this study.

Seed production was greater in provenances from both north and south of the Nanling area. Seed production was positively correlated with temperature sums at the trial sites. A similar observation has been noted in Wright (1976) for *Pinus strobus* where cone production in a provenance test was limited to the slowest growing northern seedlots.

A more extensive, nationwide study has been carried out more recently consisting of two trials (China, National Collaborative Research Group on Provenance Trial of Chinese Fir, 1988). In the first, 19 seedlots were grown for six years on 21 sites; for the second trial 43 seedlots were grown for three years on 45 sites. Again there were significant provenance differences for standing volume; the five best provenances had 3.3 times as much as the five worst (first trial). In the second trial, heights of the five best provenances were 26 % greater than the five worst. Significant and very significant correlations were found for heights at ages 4 - 7 years with those at ages 3, and 4 - 6. Correlation coefficients ranged from 0.515 - 0.675 (age 2), to 0.948 and 0.949 (age 5).

Results from these trials were used in conjunction with the earlier climatic zone and region studies to select appropriate provenances for each region. As with the Guangdong trials the best performing provenances, in terms of growth rate, adaptability, and frost resistance were those from the Nanling area. Flowering and seed production was similarly low compared with other provenances. Best provenances identified and used in this study were Rongshui and Lechang. Other provenances used in the trials and in this study were: Fujian Datian (good provenance) Hunan Huitong ("average" performance); Longquan and Anhui Huoshan (poor performing). A summary of relative performance of the various provenances tested in the above studies is given in Table 3.1.

It is clear that there is genetic variation in populations of *C. lanceolata*. The above classical field approach to provenance testing gives a practical result in terms of assessing provenance suitability for growth and productivity. Other methods such as isozyme analysis and karyotype studies also provide a measure of genetic variation. Isozyme analysis, although not as extensively used as classical field testing, has also shown some genetic differentiation between provenances. Yu and Zhang (1986) found differences among seeds from eleven provenances (including Lechang, Huoshan and Shaanxi Pingli present in this study). Differences were seen in peroxidase, esterase and α-amylase patterns; these were not related to latitude. Huang *et al.* (1986) examined esterase patterns of 63 seed sources. They identified seven types of variation and within each main centre of culture there was a dominant specific type of isozyme and variation tended to be simplified. However variation increased further away from the centres; this is similar to the breeding zones suggested by Chen *et al.* (1980). Centres of poylmorphism were found in the west and southwest of Sichuan and in southeast Yunnan, it is suggested that these are possible places where *C. lanceolata* may have originated.

Fu (1987) reported on variation in populations in Sichuan. There was a variation trend in north-south regions and differences between high and low latitude or elevation were in accordance with the north-south trend. Müller-Starck and Liu (1989a) showed significant differences between two Sichuan provenances and concluded that interpopulational variation of *C. lanceolata* is outstandingly high. Isozyme analysis has also been used to examine differences in susceptibility to squirrel damage (Huang *et al.*, 1982).

Investigation of the karyotype shows that somatic chromosome complement of *C. lanceolata* has 22 chromosomes in 11 pairs, satellite chromosomes are also observed (Han *et al.*, 1980; 1984; Kuo *et al.*, 1972; Wright, 1962). Han *et al.* (1980) examined karyotypes of *C. lanceolata* from two provinces; Hunan and Fujian. The Hunan karyotype contained supernumerary (satellite) B-chromosomes while non were found for the Fujian karyotype. Further study of 20 provenances suggested that the B-chromosome karyotype (found in five provenances) is polymorphic in nature (Han *et al.*, 1984).

Multivariate analysis identified provenances from Sichuan Dechang (southwest Sichuan) to be geographically and ecologically distinct from other provenances. This may also explain the poor performance in the provenance trials in Guangdong.

4. TREE BREEDING

In the above studies the approach has been primarily concerned with determining the extent of geographic variability and matching appropriate provenances with sites. The aim is to increase productivity (timber production). Another approach is tree breeding, with the aim of obtaining genetic improvement for various traits (*e.g.* fast growth rates, resistance to pests or disease, frost tolerance, drought resistance). Both approaches (provenance testing and tree breeding) are forms of tree improvement, but tree breeding is a more manipulative and advanced form, usually following provenance studies.

Chen and Shi (1983) discussed problems in genetic improvement of *C. lanceolata*. They noted that geographic variation was irregular and advocated short term improvement by selection of superior plantations and plus trees within sub-populations. Long term improvement by way of selective breeding was stressed (breeding populations) and was considered separately from production "populations" (seed production). Further work (Chen and Shi, 1984) examined mating designs, intraspecies heterosis, use of early selection in prediction of improvement, and genotype x environment interaction (GEI) in progeny testing.

4.1 Progeny Trials

Earlier work by Ye *et al.* (1980a) showed a highly significant effect of GEI in a half-sib progeny test on five year old plants from 45 families. The GEI effect was comprised of the following components; family x year (7.36 % of variation), family x site (7.39 %), and family x site x year (17.91 %). Accordingly GEI patterns need to be explored when considering breeding programs. Analysis of a multiplantation progeny test (half- and full-sib tests) also showed a highly significant effect of GEI; family x site interaction was 10 - 20 % of total variance (Ye *et al.*, 1980b). Rankings of the best families did not differ greatly between years, correlation coefficients were 0.742 and 0. 792 for rankings at age 1 year and ages 2 and 3 years respectively. In both tests there were significant family differences in height growth and families were then classified according to four classes; fast growth, medium, variable, and slow growth.

In other work GEI was highly significant (6 % of total variance) for raw height or log transformed height (Wang, unpubl.), but there was no effect of site x year for transformed height or family x year for raw and transformed height. Annual increment between ages three and five were similar for all families and rankings remained stable

(within each plantation). Selection for fast juvenile growth was considered feasible at age three.

Growth of 100 progenies (from natural pollination in the Guangdong seed orchard) of *C. lanceolata* at six sites in Guangdong was assessed (Guangdong Progeny Test Cooperation Group of Chinese fir, 1986). Twenty selected varieties (possibly the top twenty, but not specified in translation) had on average 11 % greater height growth, 13 % more breast height diameter growth, and 37 % more in timber volume than the control. Progeny of open pollinated plus trees had 20 - 30 % greater volume than the parents by age 7 years and height growth was 18 % more after age 2 years (Nanking Forest Products Industrial College, 1977). Estimates of heritability were high; 47 - 88 % for height increment, and 27 - 72 % for diameter growth. Similar genetic gains were found in another study of open pollinated seeds from plus trees (Chen *et al.*, 1985). Expected genetic gains after 20 years were 18 % for height and diameter and 30 % for volume; realised gains were slightly below these estimations.

Significant differences among families were found for diameter and height growth from a trial of 347 open pollinated plus tree families (Li *et al.*, 1990). Differences among families were due to both provenance and individual differences and therefore individual tree selection was considered effective.

Full-sib progeny tests have also been carried out (Chen *et al.*, 1982; Ye *et al.*, 1981b) with emphasis on combining abilities (general and specific). Factorial, half diallel, and complete diallel mating designs were also evaluated (Ye *et al.*, 1981b); recommendations as to the appropriate design for either commercial use or theoretical research are given in Chen and Shi (1984).

General and specific combining abilities (GCA and SCA) and reciprocal effects were highly significant for height growth (Ye *et al.*, 1981b). At age 4 years narrow sense (additive genetic variance) heritabilities were high (0.86 for family, 0.35 for individual trees). Height growth from seedling to age 4 years showed that SCA (non-additive genetic variance) effects accounted for most of the total genetic variance at the seedling stage (34-83 %), declining with age. GCA effects conversely increased with age. Selfing effects also varied according to parent.

Heterosis (or hybrid vigour) was studied in six parents from plus tree clones (Chen *et al.*, 1982); 23 % of crosses exceed their parents in height growth. Combinations of parents with high SCA and similarly combinations of parents with high GCA did not directly result in good seedling height in their progenies. The level of heterosis was therefore a result of interaction of GCA, SCA and in particular, reciprocal effects. Estimates of narrow sense family heritabilities were: 0.74 for height, 0.34 for number of branches,

0.43 for number of whorls, 0.11 for length of longest branch. Root collar diameter was not under control of GCA, SCA or reciprocal effects.

The high (family) heritability for seedling height indicates that direct selection of seedlings by mass selection is likely to be efficient. As with Ye *et al.* (1981b), selfing produced variable results. In height growth some individuals showed no inbreeding depression, it was suggested that those parents which did not produce seedlings with depressed height had high GCA. A study of progeny from (randomly pollinated) seed collected from dominant trees showed that genotype was consistently related to phenotype (China, Elite Breeding Section, Forestry Institute of Kaihua County, 1988), which further supports mass selection. Early selection was considered reliable by Ye and Chen (1981). Height, diameter and volume growth measurements from a progeny test were closely correlated (to successive years growth) between ages 1 - 16 years both within and between families. Selection at ages 6 and 7 years was estimated to give 60 % greater (genetic) gain than selection at 25 years (Ye and Chen, 1981).

4.2 Seed Orchards and Genetic Gains Achieved From Orchard Seed

Clonal and seedling seed orchards have been established *e.g.* Yangkou Forest Farm and Guanzhuang Forest Farm in Fujian, and in Hunan. Site selection of seed orchards is important (Chi, 1988); analysis of 28 orchards in 6 provinces showed that sites in the central region produced seeds of lower quality in the early years of production compared with those in the north region. Lower quality was probably due to excessive precipitation during pollination and drought during seed development.

Estimates of genetic gains from both types have been made (Ye *et al.*, 1981a). Offspring from the clonal seed orchard produced 33 - 72 % more volume growth than control trees, compared with 14 - 39 % from offspring of phenotypically superior mother trees. For first generation clones genetic gains were estimated to be: Height, *ca.* 7 %; diameter, 19 - 20 %; volume, 27 - 28 %. While volume growth was greater in clonal seed orchard progenies, a genetic gain of 20 - 26 % for diameter was estimated for first generation seedling seed orchard progeny. In that study further selection of second generation parents was made from the progeny tests. In Yangkou Forest Farm, a 13 year old stand from a first generation seed orchard had 33 % more volume than control stands and in Guanzhuang Forest Farm, a 7 year old stand from a first generation seed orchard had 44 % more volume than control stands (China, Forestry Sector Loan Project, 1989a).

Wood properties of progenies from an open pollinated seed orchard were investigated (Ye and Zhang, 1987; Shi *et al.*, 1987). Within tree variation of specific gravity (SG) and tracheid length was significant and there was high correlation between juvenile (5, 10, 15 years) and mature (28 years) phenotypes for both traits. Correlation coefficients ranged from 0.57 - 0.99, correlations were more accurate with increasing age (Ye and Zhang,

1987). Significant family differences were found for SG and heritability estimates were 0.29 for individual and 0.50 for family (Shi *et al.*, 1987). It was considered possible to select for early rapid growth and high SG although correlations between SG and volume were weak, however correlations between SG and other wood properties (modulus of rupture, modulus of elasticity, maximum crushing strength, impact bending strength) were high (0.73 - 0.92). Thus selection for improvement of juvenile wood with high SG and resulting good mechanical properties can be made.

4.3 Genetics of Sexual Reproduction

As mentioned in section 4.2, isozyme studies have been carried out on *C. lanceolata*. In other work Müller-Starck and Liu have used isozyme analysis to characterise genetic structure and describe mating systems (1988, 1989b). As a preliminary step to subsequent analysis of inter and intra population variation, six enzyme systems were examined in seeds from single maternal clones (Müller-Starck and Liu, 1988). The six enzyme systems were coded for by ten loci, and interactions were analysed from gametic segregation (analysis of haploid endosperm and diploid embryo tissue). A considerable number of codominant alleles were observed; null alleles were also observed although at very low frequencies (around 1%). There was a large amount of variation in recombination frequencies, and linkage between GOT-A (glutamate oxaloacetate transaminase), GOT-B and PGI-A (phosphoglucose isomerase) was inferred, consistent with findings in other conifers. In another isozyme study similar variation in recombination frequencies was reported among clones and 5 linkages between various loci were found (Geburek and Wang, 1990), six enzyme systems out of nine were highly variable.

In large populations reproduction is assumed to occur through random mating (Hardy-Weinberg), deviations from this system can arise for a number of reasons. Three types of mating systems for two Sichuan provenances were examined; Hardy-Weinberg, multiplicative (random association encompassing sexual asymmetry of gametes), and inbreeding (Müller-Starck and Liu, 1989b). Results indicated that inbreeding was favoured over the other systems. However other phenomena may have also contributed to the observed large number of homozygotes (*e.g.* environment-dependent viability selection, genotype-dependent differential self-fertilisation). A similar tendency was seen in another species of the Taxodiaceae, *Sequioadendron giganteum* (Finns and Libby, 1982). It was suggested that if inbreeding was the dominant mating system, this would most likely occur through small sized inbreeding-effective neighbourhoods (Müller-Starck and Liu, 1989b). This in itself is not necessarily bad as selfing (extreme form of inbreeding) produces variable results and depends upon the parent's GCA; those with high GCA may not exhibit inbreeding depression.

Seed from a clonal seed orchard has been classified into three types according to vigour: Healthy, containing tannin-like substance, and empty (Ye *et al.*, 1981c). Variation in seed vigour was highly significant, with significant family differences for production of healthy and tannin-like substance seeds. Seed vigour is affected by both SCA and GCA, with SCA showing high heritabilities (0.47 - 0.67 for individual, 0.93 - 0.97 for family). Selfing effects were the main factor in determining the amount of seeds containing tannin-like substance.

Other genetic related research has been carried out. Karyotype analysis has already been described above in terms of provenance variation, chromosome banding using Giemsa C-banding method has also been investigated (Xiao and Liao, 1986; Tong and Hao, 1986; Chen and Fang, 1990). Chromosome banding is used in gene mapping, however while Giemsa C-banding produces clear bands no recent work appears to have carried out actual mapping.

5. SUMMARY

C. lanceolata has a wide planted geographic distribution with a large variation in climates and topography. Growth has been correlated with such factors as latitude, rainfall and relative humidity. Provenance tests have been extensively and intensively carried out for a number of years and show significant provenance differences in growth, frost resistance and seed production. In most tests, provenances from the Nanling ranges and Fujian are usually considered the best performing provenances, at least in terms of growth.

Provenance tests have been carried out in part to match appropriate provenances with sites; and site classification and provenance selection is now well documented. Tree breeding programmes have also been implemented and results show that improvements over natural open pollinated stock are significant, in terms of growth and wood properties. Heritability of height growth, in particular, and also of diameter and volume appears to be very high and therefore early selection for juvenile fast growth is feasible. Seed orchards have also been established and contribute up to 30 % of seed for annual plantings; both seedling and clonal seed orchards are used. Improved first generation and second generation seed orchards have been established, indicating that the breeding program is well advanced.

Other research on genetic aspects has similarly shown genetic variation to exist. Differing karyotypes from different areas have been found and isozyme analysis has shown regional differences. These findings appear to agree with the more conventional provenance tests. The reproductive process has also been examined with isozyme

analysis and findings indicate that inbreeding is probably the dominant form of mating system.

Table 3.1: Relative Performance of Various Provenances

Rank	Biomass[1]	Height (5 yr)[1]	
1	HU, Jianghua	SX, Hanzhong	a
2	**HU, Huitong**	FJ, Shunchang	ab
3	FJ, Shunchang	HU, Jianghua	abc
4	SX, Hanzhong	**GD, Lechang**	abc
5	**GD, Lechang**	GZ, Tianzhu	abc
6	GZ, Tianzhu	JX, Dingnan	bc
7	JX, Dingnan	**GX, Rongshui**	bcd
8	**GX, Rongshui**	ZJ, Lishui	cd
9	ZJ, Lishui	**HU, Huitong**	cd
10	JS, Yixing	JS, Yixing	d
11	SC, Yichang	SC, Yichang	d

	Volume (9 yr)[2]		Volume (6 yr)[3]	Zone Suitability[3]
Best	**GX, Rongshui**	Best	**GX, Rongshui**	I_1, I_2, II_1, II_2, II_{3a}
	GD, Lechang		**GD, Lechang**	I_1, I_2, II_{3a}, III
	GZ, Jinping		**HU, Huitong**	I_1, II_1*, II_2
	FJ, Jian'ou		GZ, Jinping	I_1, II_1, II_2, II_{3a}, III
	HU, Jianghua		HU, Jianghua	I_2, II_1, II_2, II_{3a}
	JX, Quannan		JX, Quannan	I_2, II_1, III*
	SC, Jianwei		FJ, Jian'ou	I_2, II_2, II_{3a}, III
Poor	AH, Yixian		HB, Enshi	I_1
	ZJ, Kaihua		SC, Qianwei	II_1*, II_{3b}*
	ZJ, Longquan		Native Prov's	II_{3c}
	SC, Dechang			

n.b. **Provenances in bold are represented in this study.**

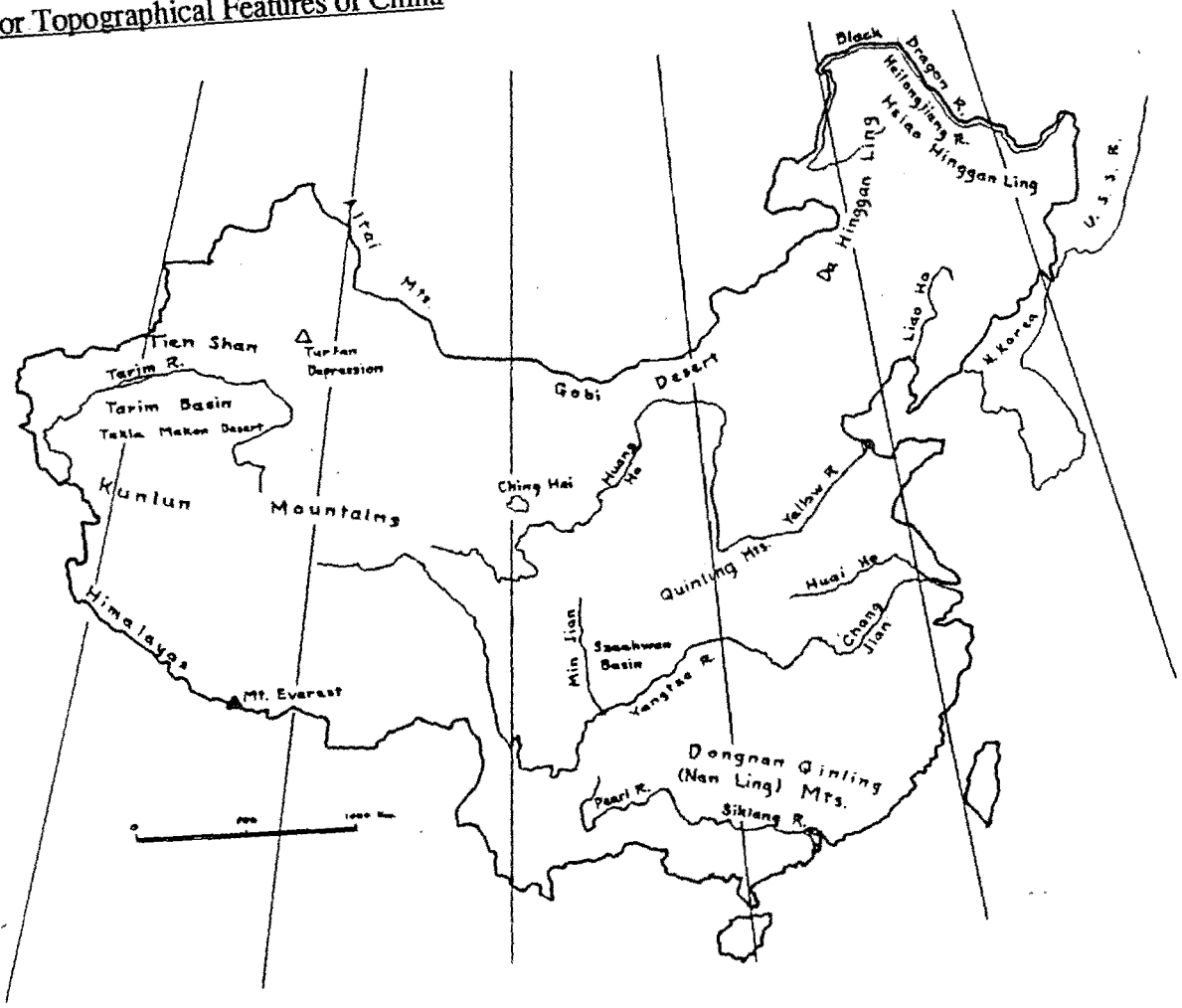
[1] Chen *et al.*, 1980; significance test is for height only (Tested in Fujian).

[2] Guangdong Prov. Trial Coop on Chinese fir, 1986 (Tested on various sites in Guangdong).

[3] Nat. Collab. Res. Group on Prov. Trial of Chinese fir, 1988 (Nationwide trial).

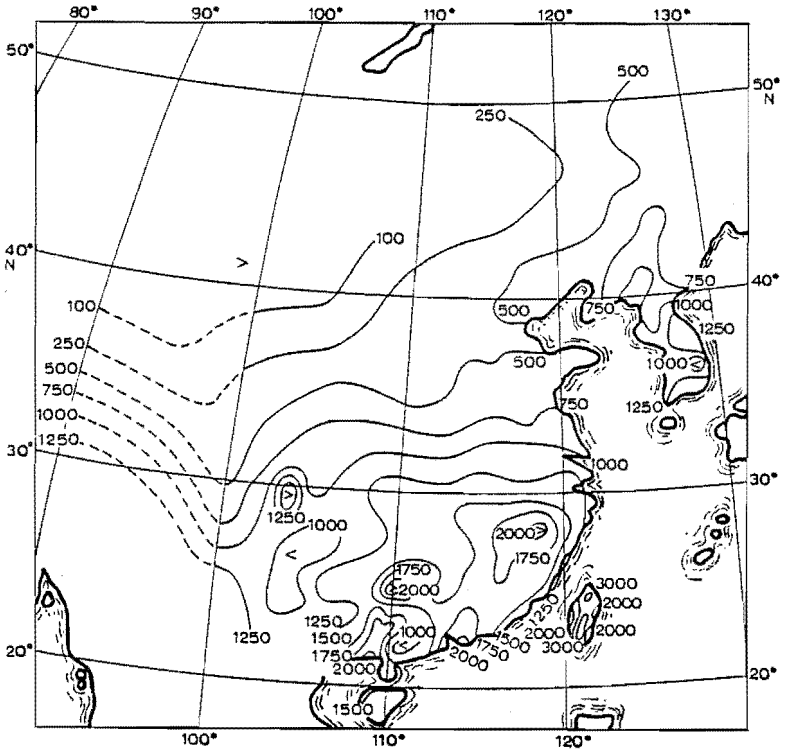
* For use on poor sites.

Figure 3.1: Major Topographical Features of China



(From FAO, 1982)

Figure 3.2: Mean Annual Rainfall (mm)



(From Watts, 1969)

Figure 3.3: Seasonal Rainfall of Sample Sites

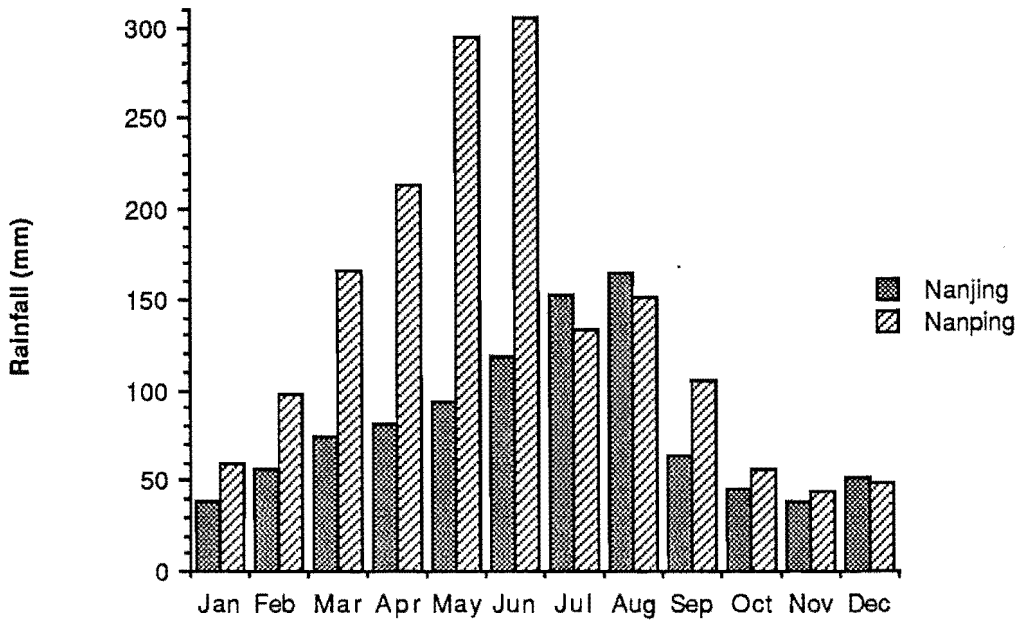


Figure 3.4: Seasonal Rainfall of Sample Sites

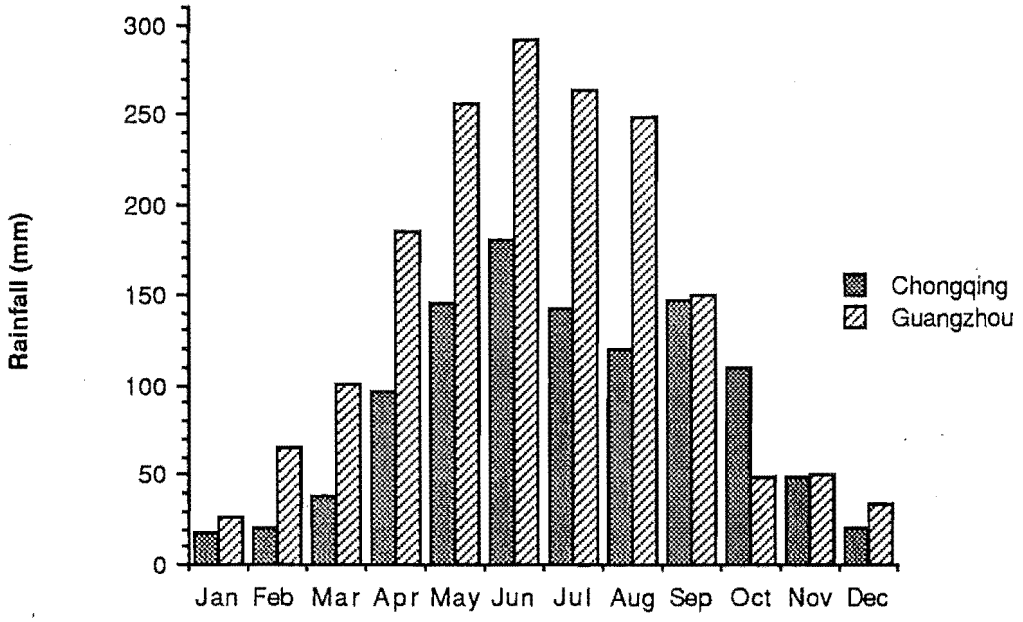
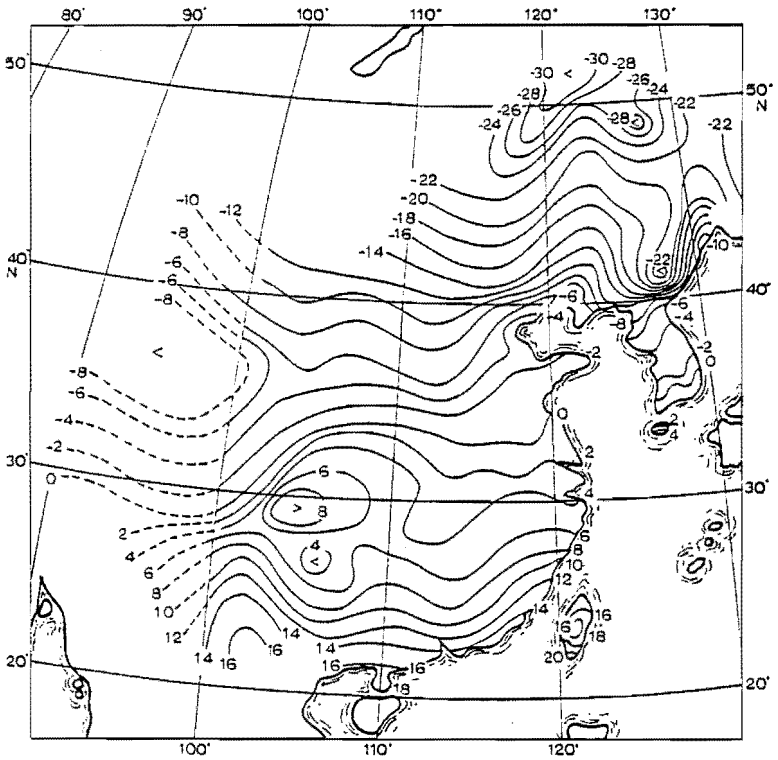
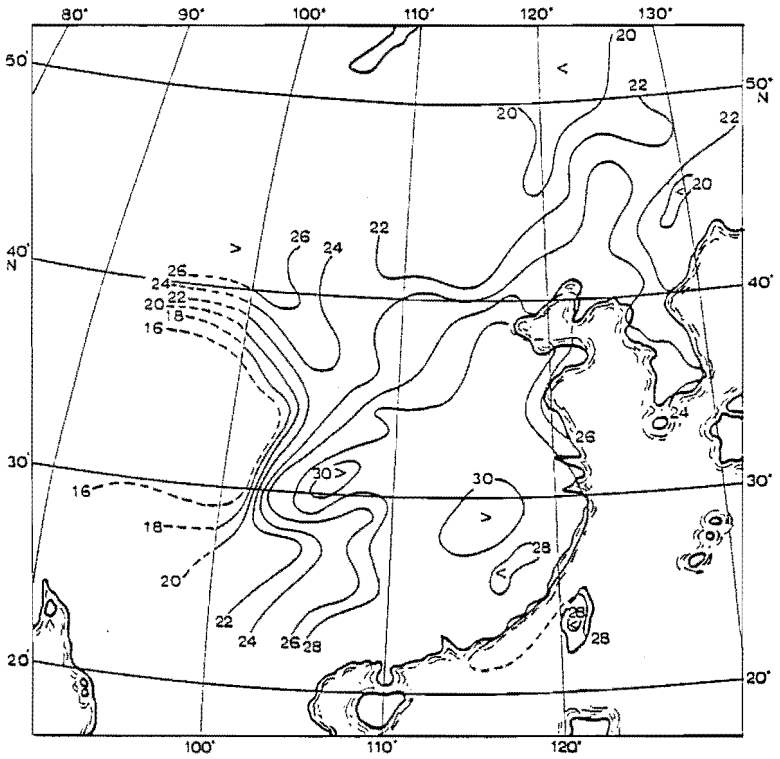


Figure 3.5: Mean Air Temperature in January (oC)



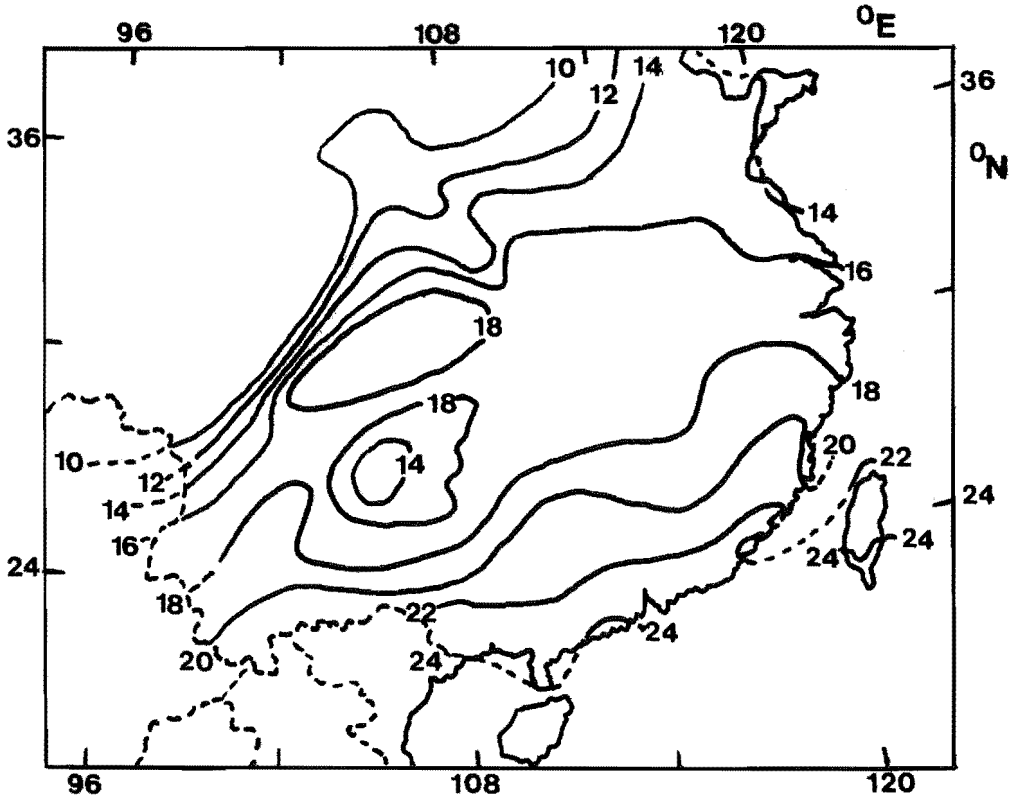
(From Watts, 1969)

Figure 3.6: Mean Air Temperature in July (oC)



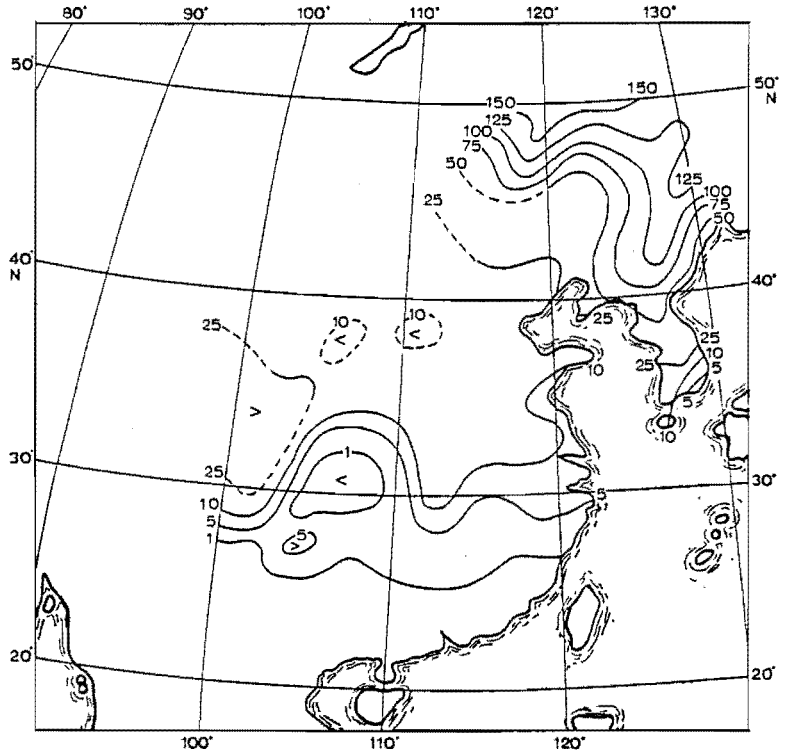
(From Watts, 1969)

Figure 3.7: Mean Annual Air Temperature (oC)



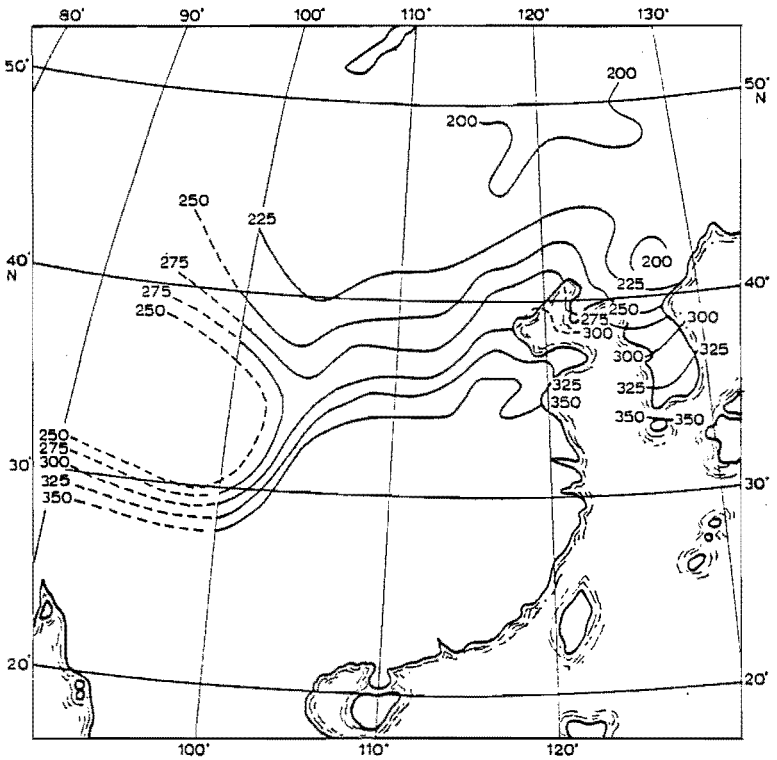
(From Hsieh, 1973)

Figure 3.8: Mean Duration of Snow Cover (days)



(From Watts, 1969)

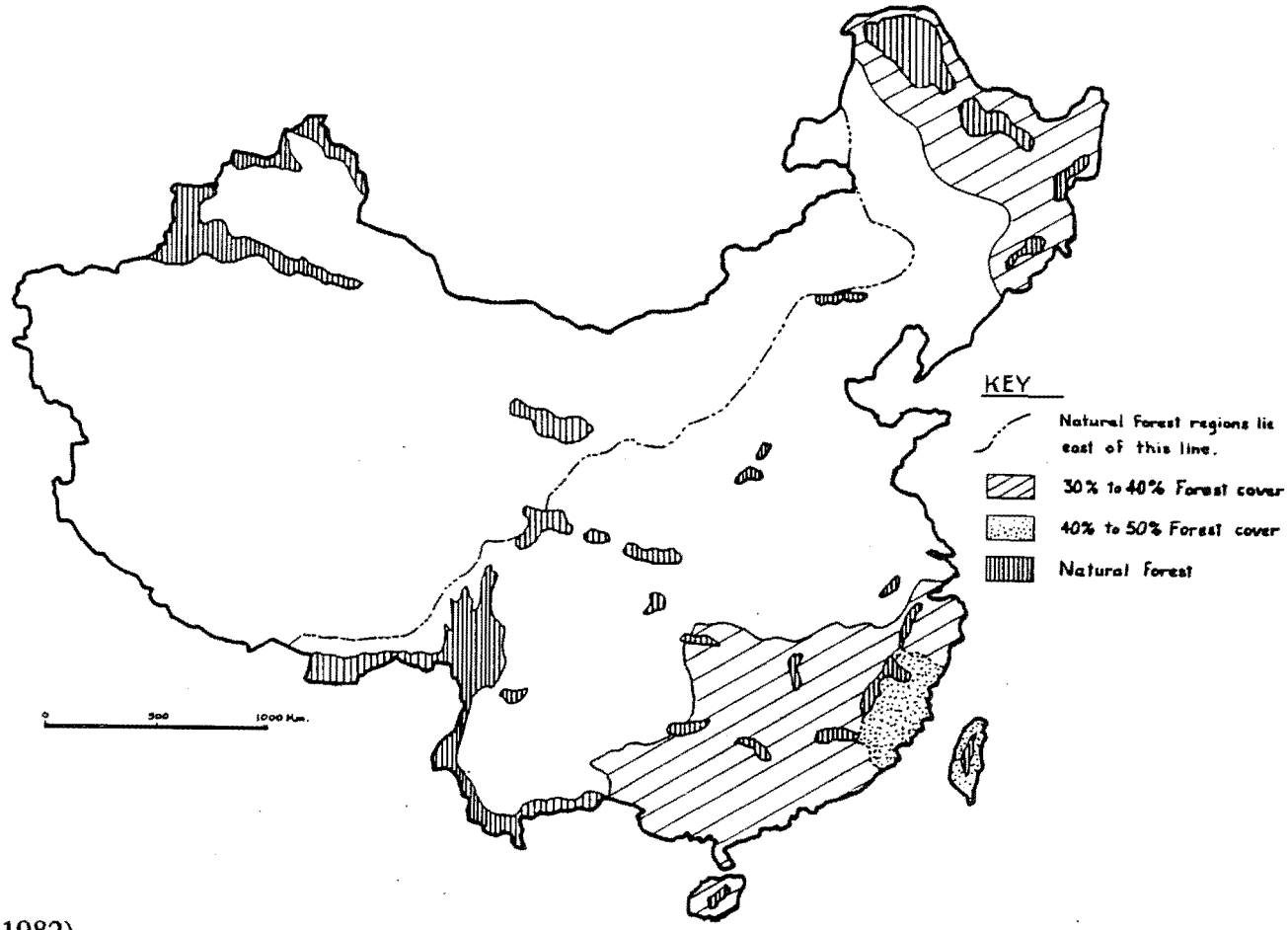
Figure 3.9: Mean Number of Days Above 0 oC



(From Watts, 1969)

Figure 3.10: Natural Forest Cover in China

(note *C. lanceolata* distribution approximatetly corresponds to 30 - 40 % forest cover region in south east)



(From FAO, 1982)

CHAPTER IV

A NURSERY TRIAL OF THE ELEVEN PROVENANCES

1. INTRODUCTION

Nursery trials are an important aspect of provenance testing. While field trials ultimately determine the suitability of particular provenances to particular sites, nursery trials can provide an initial indication of likely variation. In addition, early measurements and observations allow the examination of early height relationships changing with age (Sweet, 1965).

Heights of 16 year old *P. strobus* showed only a moderate correlation (r = 0.33 - 0.58) with 2 year old nursery heights (Genys, 1987); diameters at age 16 years were similarly correlated to 2 year heights (r = 0.38 - 0.61). Stronger correlation was found to exist with later (age 10 years) measurements. However for *C. lanceolata* it does appear that there are strong correlations of early and later growth; in provenance trials significant correlations were found between ages 2 - 5 years (Chen *et al.*, 1980), and 3 - 9 years (Guangdong Prov. Trial Coop on Chinese fir, 1986). Similarly in progeny trials, height, diameter and volume growth were closely correlated (to successive years growth) between ages 1 - 16 years both within and between families (Ye and Chen, 1981). Rankings in best performing families in a progeny trial showed significant correlations for age 1 with ages 2 and 3 years (Ye *et al.*, 1980). For details see chapter III.

Early selection is thus considered to provide a reasonably reliable estimate of growth; and selection at age 3 has been suggested by Wang (unpubl.). Thus a nursery trial of the *C. lanceolata* provenances is important to determine the extent of variation. In this experiment the eleven provenances were grown in a nursery trial for two years to assess their performances in terms of growth and phenology, and the extent of provenance variation in these parameters.

In order to maximise germination of available seed in this study, an experiment was carried out on unstratified seed to find the optimum temperature for germination.

Materials and Methods: Testing was carried out in a germination chamber with a controlled temperature gradient. Ten temperature treatments were used ranging from 13.6 to 30.2 ^{o}C. Seeds of two provenances, PV5 and PV11, were used.

Seeds were soaked in tap water for one day prior to the experiment. For each temperature treatment twenty seeds of each provenance, in two replicates of ten, were placed on moist filter paper in petri dishes. Daily observation, watering and changing of filter paper (when necessary) was made. A seed was deemed to have germinated when its root radicle was 2 mm or greater, the germinated seed was then removed from the dish.

After 26 days the experiment was halted and a tetrazolium staining test was made on the remaining ungerminated seeds to determine their viability. Numbers of germinating seeds were then converted to a percentage of sound seed and plotted against time. Numbers of sound seed in replicates ranged from 20 to 100% of total seed; some replicates only contained two or three sound seeds. Replicates for each provenance were therefore pooled within each treatment. Table 4.1 shows seed numbers in each provenance for each pooled treatment.

Germination values (GV) from Djavanshir and Pourbeik (1976), reported in Hawkins (1989) were calculated and plotted for each provenance x treatment combination:

$$GV = [(\Sigma DGS)/N)] * GP * 10$$

where DGS = daily germination speed
(cumulative % germination/number of days)
N = number of DGS's calculated
GP = percent germination at end of experiment

Results: Germination values are given in Table 4.1 and Figure 4.1. The generally higher GV's for PV5 are due to PV5 seeds germinating more rapidly at most temperatures. While no statistical significance can be calculated from these results they indicate that a broad germination temperature optimum lies between 22.8 and 26.2 ^{o}C for PV5 and between 24.6 and 27.6 ^{o}C for PV11.

Figure 4.2 shows the trend of germination over time for PV11. At lower temperatures germination is slow to start (germination occurred after 19 days at 13.6 ^{o}C and 16 days at 15.3 ^{o}C); amongst the higher temperatures initial germination rates appear to be similar, merely differing in starting times. PV5 is not shown but has a similar response to PV11. Percent germination over time is shown in more detail for the temperatures with the three best GV's for each PV in Figures 2.3 and 2.4. Slopes (rate) are similar in appearance although the slope of the temperature with the lowest GV (24.6 ^{o}C for PV5, 27.6 ^{o}C for PV11) for each PV are slightly less than the those of the two higher GV's.

SEE ERRATA

2. MATERIALS AND METHODS

Seeds from the eleven provenances with viable seed were soaked for 24 hours then stratified at 4 °C for four weeks. After stratification seeds were sown in trays containing commercial seed-raising mix, and germinated in a glasshouse at 25 °C. Eighteen days after sowing, seedlings were transplanted into root trainers and sprayed with Previcur, a damping off fungicide. Seedlings were kept in a heated glasshouse (*ca.* 20 °C), and under 50 % shade cloth.

Two months after sowing, in early October 1988, seedlings were shifted outside and kept under 50 % shade cloth for 12 - 14 days, then planted out into the prepared nursery beds. Blanking with spare seedlings was carried out up to four weeks after initial plantings. Seedlings were kept under 30 % shade cloth for wind and radiation protection until they were growing vigorously; shade cloth was then removed.

2.1 Provenance Material

All provenances represented in this study (with the exception of PV6) were used in this experiment. Details are given in appendix A. Climate data for each provenance except PV8 was collected by Mr Chen Jianxin, of FRI, Guangdong (Li, pers. comm.), data for PV8 was obtained from Wu (1984).

2.2 Nursery Layout and Design

The nursery site was formerly under grass and had been mechanically cultivated twice with mushroom compost added prior to planting. Soil tests carried out for N, P, K and pH showed acceptable levels for nursery conditions. Test results are shown in Table 4.2.

Seedlings were planted into four beds (blocks). Poor germination in some provenances meant that seedling numbers were not equal in all provenances; however numbers within provenances were consistent between blocks. Because of bed-length restrictions, provenances were arranged in columns of two within each block; provenances were randomly ordered in each block. A diagrammatic layout is given in Figure 4.5.

Seedling spacing was initially set at 10 cm x 15 cm with five seedlings per provenance per (east-west) row. Seedling numbers per provenance in each block ranged from 10 - 25. After one season's growth the blocks were thinned to three seedlings per provenance per row. Final numbers therefore ranged from 6 - 15 seedlings per provenance per block

2.3 Analysis

Height growth was recorded for the first two blocks in the first growing season, as was date of bud set. Periodic checks of height on sample seedlings were made throughout

winter (non growth season), and bud conditions noted. At the first sign of bud swelling height measurements were resumed on 5 September 1989 (week 0) for all seedlings in all four blocks. Amount of terminal (BB_t) and lateral (BB_l) bud burst was also assessed at the same time as heights were taken, as was damage to growing tips from spring frosts ($FD_{week\ 9}$).

Measurements continued until 2 May 1990 (week 34), the end of the second growing season. Bud set (BS) and frost damage (FD) assessments were made on 9 May (week 35). Seedlings were further scored for frost damage later in the winter (dormant season) on 21 August, 1990 (week 50).

Final height measurements were analysed using ANOVA and analysis of covariance as for a randomised block design. Final height was analysed in three forms: raw measurements, log transformed measurements, and raw measurements adjusted for initial height (with initial height as the covariate). The ANOVA format was as follows:

Source	Degrees of Freedom
Block (BK)	3
Provenance (PV)	10
Error	30
Total	43

Seasonal height growth was graphed in log form and in raw form. Bud set and frost damage were also compared by ANOVA.

Using provenance climate data obtained via Li Zhaobang (pers. comm.) and Wu (1984), final height, bud set, frost damage at week 35 and week 50 correlated with; latitude (LAT), longitude (LON), altitude (ALT), mean annual temperature (MAT), mean January temperature (MCT), mean July temperature (MWT), temperature sum (TSM), mean annual rainfall (MAR), mean annual sunshine hours (MAS), and frost free days (FFD). All correlation analyses had 43 degrees of freedom (df).

3. RESULTS

3.1 Bud Burst at the Start of the Second Growing Season

For all seedlings lateral buds burst preceded terminal bud burst. Because measurements were made on a weekly basis the time lag between lateral and terminal bud burst could not be directly calculated. Instead an estimate of time lag for each provenance and the species as a whole was made by graphing overall percentages and reading off the time scale for 50 % bud burst in both lateral and terminal buds. Results are given in Table 4.3, Figure

4.6. Terminal and lateral bud burst were analysed statistically for three sets of measurements (weeks 2, 3 and 4). There was a highly significant difference ($p = 0.0042$) between provenances at week 3 for lateral bud burst. PV5 had the least bud burst and was significantly less than all other PV's except PV10. For all other measurements there was no significant difference; results are given in Table 4.4.

Frosting of tips was first noted on 10 October 1989 (week 5) and became more apparent on 31 October (week 9). Blocks 3 and 4 had the highest frequency of frost damaged seedlings indicating that there was a frost gradient between blocks. Proportions of frost damage at week 9 are given in Table 4.8.

3.2 Second Year Height Growth

The growth habit of first year coniferous seedlings is commonly indeterminate and thus seedlings will grow as long as the environment is suitable (Lavender, 1984). Genetic differences in growth can then be masked by environmental conditions although relative lengths of the growing season between provenances may still be present. Second year growth is more strongly under genetic control and so is analysed in this experiment. Data for heights of first year seedlings from blocks 1 and 2 are given in Table 4.5, as well as starting heights of second year seedlings; the difference in numbers are due to the thinning carried out over the intervening winter. Significance tests shown in Table 4.5 are for the individual measurements. However when results were analysed for all four blocks there were no significant differences between provenances at either the end of the first year or at the beginning of the second.

Height growth for the species as a whole followed a typical sigmoid growth curve (Figure 4.7). The growing season for height in the second year lasted about 34 weeks, from early September through to the beginning of May. Final heights for each provenance are shown in Table 4.6 and an indication of height growth mid way through the growing season is shown in Plate 4.1. ANOVA of final height measurements (week 34) showed no significant differences between provenances. There was a highly significant block effect and this was clearly visible in terms of height growth, bud set and frost damage. Analysis of covariance showed significant differences between PV4 (best), and PV5 and 11 (worst). Otherwise there were no differences among provenances although rankings differed slightly to those obtained through ANOVA. Results are shown in Table 4.6, significance is shown in Table 4.7.

Interestingly spring frost damage was most evident on the "southern provenances (PV's 1 - 4 and PV's 11 and 12), although this was not significantly different from other provenances. While this would have resulted in reduced growth in the badly affected seedlings, overall growth (at least for PV4) did not appear to be greatly affected. Spring frost was noted at week 9, but by week 11 many buds that had been frost damaged had

resumed growth, in some seedlings lateral buds assumed dominance and became terminal shoots.

Correlation analyses of final height with climate variables showed no significant correlations (r = 0.009 to 0.069, p = 0.4145 to 0.9594). Results of these and bud set and frost damage correlations are given in Table 4.9.

3.3 Bud Set After the Second Growing Season

Terminal bud set was noted in a few seedlings as early as week 28, mostly occurring in block 1. Terminal bud set was measured weekly from week 30 to week 35, and lateral bud set from week 32 to 35. Seedlings were subject to frosts from week 32 onwards and this effectively prevented further appreciable (terminal) bud set due to damage to apical tissue, although some seedlings continued to develop buds.

In contrast to bud burst, terminal buds formed first, then lateral buds. In the species as a whole, lateral bud set lagged behind terminal bud set by approximately 10 days (Figure 4.8). However there were significant differences between provenances in proportion of (terminal) buds set at week 35 (Table 4.8, Figure 4.9). Those provenances which had low bud set were "southern" provenances (PV1, 2, 3, 11). In general provenances with high bud set were "northern" (PV8, 9, 10) although a more southern and interior provenance, PV5, had the highest bud set. Correlation analysis of bud set with LAT was significant as were correlations with MAT, MCT, TSM, and MAR. There were no significant correlations with LON or ALT. Results are given in Table 4.9.

3.4 Frost Damage After the Second growing Season

Frost damage was first recorded on 25 April 1990 (week 33), grass temperature recordings near the nursery plots showed that several frosts had occurred in the previous week on 19, 20, and 23 April (-3.5, -1.5, -0.5 ^{o}C respectively). Damage became more widespread over time and on the final measurement of the second growing season on 9 May (week 35), damage was inversely related to bud set, *i.e.* those provenances with high bud set had low frost damage (Figure 4.9). This was clearly due to soft (growing) bud tissue being exposed to freezing conditions in plants which had not formed protective over wintering buds. Ranking of frost damage was therefore almost exactly opposite to that of bud set (Table 4.8). Correlation analysis between frost damage and bud set at week 35 was significant at 0.01 % with the coefficient r = -0.924 (43 df). Significant provenance differences in frost damage were similarly observed.

Almost one year after the start of the second growing season and prior to the start of the third growing season (week 50), a final frost damage score was made to see if further damage had occurred over winter. Typical damage is shown in Plate 4.2. Results showed that damage had increased, but overall ranking remained relatively unchanged

(Figure 4.10). The correlation coefficient between frost damage at week 35 and week 50 was: r = 0.899 which was significant at 0.01 % for 43 df.

Correlations with climate variables were stronger at week 50 than week 35. Significant correlations were found at week 35 with LAT, MAT, and TSM; and at week 50 with LAT, MAT, MCT, TSM, and MAR. Results are in Table 4.9.

4. DISCUSSION

4.1 Bud Burst

Because weekly measurements of all seedlings were made (rather then daily measurements) statistical analysis did not show any significant differences in bud burst other than lateral bud burst in week 3; this suggests that bud burst occurs fairly uniformly over all provenances within this time period (one week). Differences may be apparent in terms of days but this could not be statistically shown here. Interpolation of bud burst data as seen in Figure 4.6 and Table 4.3 suggests that *C. lanceolata* is relatively uniform in timing of bud burst and lag time between lateral and terminal bud burst. The range of median (50%) burst times, for the eleven provenances, was 8 days for lateral buds and 4 days for terminals. In comparison *Pseudotsuga menziesii* was 26 and 30 days respectively for 30 provenances (Sweet, 1965). Similarly time lag was 3 - 8 days for *C. lanceolata* and 1 - 23 days for *Pseudotsuga menziesii.* While the comparison is dependent upon the number of provenances used, the provenances in this study represent the latitudinal range of *C. lanceolata.*

It appears that there is very little (if any) provenance variation in terms of commencement of growth, although light spring frosts affected some provenances more than others. In another study of seasonal shoot growth, a north-south trend was observed in *C. lanceolata* provenances with bud burst occurring up to 17 days earlier in southern provenances (Yu, 1964). More discussion on bud burst timing is given in chapter XII. In the absence of detailed climate data no definite conclusions can be drawn but perhaps the change from winter to spring in sub-tropical China is more sharply defined and uniform than in temperate zones. In the range of *C. lanceolata* plantings frosts are rare from spring through summer. This would suggest that the timing of bud burst is not crucial in terms of avoiding spring frosts that slow growth or kill the plant, in contrast to the situation with *Pseudotsuga menziesii* (Sweet, 1965; White *et al.*, 1979).

4.2 Second Year Height Growth

That final growth was not significantly different between provenances (from ANOVA) is somewhat surprising given previous work on *C. lanceolata* provenances in China (*e.g.* Chen *et al.*, 1980; Chen and Shi, 1983; Pan *et al.*, 1983; National Collaborative Research

Group on Provenance Trial of Chinese fir, 1988) and a general expectation that species with a large geographical distribution tend to exhibit provenance variation (Wright, 1976). Similarly the differences in growth from ANCOVA did not demonstrate any logical trend in terms of latitude or altitude (PV's 4, 5, and 11 are from similar latitudes and altitudes).

As noted in chapter I, section 2.1, there was a no knowledge of seedlot collection details. If seedlots were representative of true provenances a general trend of differences from south to north would be expected, given that climate differences are more pronounced in this direction. Growth period in China for PV's 9 and 10 is between 200 - 245 days while for PV's 1, 2, 3, 11 and 12 it is 260 - 320 days (China, Cooperation Group of Chinese fir, 1981b). Furthermore Chinese provenance trials have consistently identified provenances from the Nanling ranges (PV's 1, 2, 3, 4, 5, 11, 12) as being the faster growing provenances (Chen *et al.*, 1980; Guangdong Provenance Trial Cooperation of Chinese fir, 1986; National Collaborative Research Group on Provenance Trial of Chinese fir, 1988). Height growth at the seedling stage was negatively correlated with latitude (Chen *et al.*, 1980; Pan *et al.*, 1983) and longitude (Chen *et al.*, 1980).

There are a number of possible reasons as to why no large differences were observed. If seedlots were not representative of true provenances, then this may serve to reduce differences. The seedlots corresponding to the provenances reported in Chinese trials may merely be from the same general area, and not representative of those reported in the literature.

While differences may be apparent in Chinese trials, site often influences provenance performance (Wright, 1976). Thus climate and site conditions in Christchurch may have served to reduce or mask growth differences. Similar examples in other conifer species are reported in White *et al.* (1981). Date of bud burst in *Pseudotsuga menziesii* was genetically different in Pacific Northwest trials (White *et al.*, 1979), while there were no provenance differences in Rotorua (Sweet, 1965).

Seedling age may also be a contributing factor. First year growth in most coniferous seedlings is typically indeterminate (Lavender, 1984) and can be influenced by germination rate (Sweet, 1965). In the second year, genetic control is more strongly shown and growth pattern moves to a determinate growth habit (Lavender, 1984), where this is a component of the species' growth pattern. From previous work on *C. lanceolata*'s growth pattern it is known that the species exhibits both predetermined (or fixed) and neodetermined (or free) growth in one season (see chapter XII).

Seedlings in their second year, as used here, are usually better indicators of genetic variability. However differences, if any, may be more pronounced in later years. In addition growth in subsequent seasons (not assessed) would be affected by frost damage

in the previous autumn and spring. While spring frost did not prevent growth, it may well have slowed potential growth. If this was the case PV4 may well have the potential for greater growth in the absence of spring frost or when terminal buds were above the frosting zone.

4.3 Bud Set and Frost Damage

Bud set is clearly related to latitude and, with the exception of PV5, follows a trend of increasing bud set (at week 35) with increasing latitude; this suggests that the seedlots used were real provenances. "Northern" provenances (PV's 8, 9 10) tended to form buds earlier than the "southern" ones (PV's 1, 2, 3, 4, 11, 12), perhaps reflecting the shorter growing season (China, Cooperation Group of Chinese fir, 1981b; Li, pers. comm.). This did not appear to relate to height in the current growing season however, as there was no correlation with FFD; and northern provenances (with fewer FFD's) were not significantly different in height, as has been discussed. Sub-tropical China has winters which are cold and relatively dry; dormancy (and hence bud set) then would most likely be induced by lowering temperature and/or drier conditions (Golfari, 1963). Although dormancy protects against cold and drought, this does not necessarily mean that these factors act as triggers for dormancy; dormancy issues are examined in chapter XI. Evidence for provenance variation in either bud set or timing of dormancy has been shown in Yu (1964), and Hwang and Sun (1986) in chapter XII.

The highly significant correlations of bud set with LAT, MAT, MCT, and TSM indicate that temperature is linked with bud set. Temperature isotherms, especially winter temperature (MCT), closely follow latitudes (see chapter III) as does photoperiod. Lowering temperatures are most likely to stimulate initiation of bud set; winter temperatures in the north are colder than in the south (Watts, 1969). Northern provenances may therefore be more sensitive to lowering temperature and initiate bud set earlier. Photoperiod is responsible for bud set in many temperate conifers (Kramer and Kozlowski, 1979; Lavender, 1984). In China the maximum day length in summer (14:06 hours:minutes) differs by just over four hours from minimum day length in winter (9:54) at the most northern limit of *C. lanceolata*. At 25 ^{o}N latitude, the southernmost distribution of the provenances in this study, the difference in daylengths is just over three hours (13:33 in summer, 10:27 in winter). This may still be enough for a photoperiod effect, as Kramer and Kozlowski (1979) report that many tropical species increase growth in response to longer than normal photoperiods; however conversely some temperate species cease growth well before days begin to shorten. Other work in this study failed to identify photoperiod as having any effect on growth, while low night temperatures appeared to be a major factor in bud formation in growth cabinet experiments (see chapter XI). It would seem then that photoperiod is not likely to be a large influence on bud set of *C. lanceolata*.

A highly significant (negative) correlation was found between bud set and MAR indicating that seedlings of provenances from low rainfall areas set buds earlier. Rainfall itself was not a direct factor in bud set; Christchurch rainfall pattern is comparatively uniform (N. Z. Met. Ser., 1980) and seedlings were kept well watered up to the end of the growing season. It is therefore unlikely that water deficit would induce bud set directly, at least for PV's 5, 8 and 10, but it would seem that there is some genetic control over early bud set as a result of adaptation to drier areas. It is possible that this correlation is due to the relationship between rainfall and latitude (see chapter III) where rainfall decreases from the southeast to the northwest. The correlation with MAR therefore may not be as appropriate as with LAT.

As noted earlier, frost damage was inversely related to bud set. Thus southern provenances that were still "growing" (albeit slowly) and had not yet set buds were most severely affected by autumn frost. Subsequent winter frosting tended to accentuate damage suggesting a relationship between the timing of bud set and overall winter frost resistance in the provenances. In the previous winter first year seedlings were unaffected by frost damage, mid winter frost hardiness assessments showed that the species as a whole could tolerate frosts of -15 ^{o}C with minimal damage (chapter VIII).

Frost damage in the second year was more pronounced, perhaps indicating more of a genetic influence on hardening than in the previous year. Damage was mostly restricted to the terminal and lateral shoot tips (see Plate 4.2). Phenology has been found to be important in cold resistance of other species (see chapter VIII) and although there is little difference in mid-winter frost resistance if hardening processes are allowed to proceed, provenances which have slower rates of hardening are more susceptible to late autumn frosts and may then have the hardening process disrupted. That those provenances with lower bud set suffered greater frost damage is consistent with hardening processes: The major factor in induction of frost resistance is cessation of growth (Weiser, 1970); thus those provenances with longer growing seasons (as indicated by larger FFD, MAT, MCT, TSM values) would be expected to cease growth (as evidenced by bud formation, and to begin hardening) later. It is not clear as to how the damage would affect the subsequent season's growth, light spring frosts would be expected to have more of an impact as these would kill leaf primordia and stem units laid down over winter. However autumn damage was more severe and widespread than the previous spring frost damage. Whether this would result in a delayed bud burst or not could not be assessed in this trial.

If damage was to reduce the next season's growth this would most affect the southern provenances. It would therefore be possible for growth differences to become apparent as northern provenances (and PV5) either burst earlier and/or grow faster being able to utilise both predetermined growth and food reserves stored over winter. Although the species is sensitive to out of season frosts (in particular early autumn frosts; Dallimore

and Jackson, 1931; Richardson, 1966), when branch tips are killed, cork cells develop at the seat of the injury and dead tips are then shed and new growth is produced from an adventitious bud from the healed tip (Dallimore and Jackson, 1931; Richardson, 1966); this ability is not found in other conifers. Thus growth, albeit restricted, can still occur.

Interestingly PV4 which had the greatest height growth did not significantly differ in frost damage from PV5 and the northern provenances. This may indicate that PV4 and/or the northern provenances (PV's 8, 9, 10 and 7) would be more suitable for New Zealand conditions where out of season frosts are more common than in China where southern provenances (including PV's 4 and 5) are the preferred provenances.

5. SUMMARY

From this trial there is no evidence to suggest that large provenance variation exists in terms of bud burst and height growth, at least in the nursery stage of growth. It is possible that provenance differences in growth may be more apparent in later stages, particularly if this depends on a provenance's ability to set bud before onset of autumn frosts (and thus avoid damage).

Bud set at the end of the growing season and subsequent exposure to frosts does show significant provenance differences. This, in the absence of measurable early (second year) growth differences, may be a more useful criterion for assessing provenance suitability for New Zealand climate conditions. Provenances which set bud earlier are not as badly damaged by autumn and winter frosts, this may then have some bearing in the next season's growth as bud burst is less likely to be retarded. Northern provenances appear to set bud earlier and would seem to be more suitable in this respect.

However there is still a need to establish long-term field provenance trials in New Zealand, if foresters seriously consider establishing the species here.

Table 4.1: Seed Numbers and Germination Values (GV)

Temp. (°C)	PV5 #Sound	PV5 % Germ	PV5 GV	PV11 #Sound	PV11 % Germ	PV11 GV
13.6	5	100.0	2353.06	9	33.3	319.02
15.3	9	77.8	3409.23	11	63.6	1084.44
17.3	10	80.0	3062.22	15	86.7	3033.75
19.1	7	57.1	2300.40	15	93.3	4106.85
21.0	11	72.7	3505.04	15	86.7	4398.66
22.8	14	92.9	8158.12	12	83.3	4147.00
24.6	8	100.0	7766.73	11	100.0	5487.20
26.2	8	87.5	8039.93	14	100.0	5401.33
27.6	10	80.0	6039.68	15	93.3	5184.91
30.2	9	100.0	6139.22	10	80.0	2513.88

Table 4.2: Soil Tests

Sample:	1	2	3	Compost	Douglas fir[1]
Total N (g/100g soil)	0.41	0.34	0.33	0.51	0.18-0.23
Olsen P (ppm)	42	21	18	80	25-50
Exchangeable K (g/50 000g soil)	29	28	23	60	not given
pH	6.20	5.83	5.67	6.34	5.0-6.0

[1] Recommended levels (Youngberg, 1984).

Table 4.3: Estimated Date of Bud Burst For 50 % of Seedlings (1989)

	Lateral	Terminal	Time lag (days)
PV1	26 Sept	1 Oct	6
PV2	23 Sept	30 Sept	7
PV3	22 Sept	30 Sept	8
PV4	23 Sept	30 Sept	7
PV5	29 Sept	1 Oct	3
PV7	27 Sept	1 Oct	5
PV8	27 Sept	30 Sept	3
PV9	26 Sept	1 Oct	6
PV10	25 Sept	31 Sept	6
PV11	26 Sept	2 Oct	7
PV12	27 Sept	31 Sept	4
Range (days)	8	4	3-8
All PV's	26 Sept	31 Sept	5

Table 4.4: Proportion of Terminal (BB_t) and Lateral Bud Burst (BB_l), 1989

	Week 2		Week 3		Week 4	
	BB_t	BB_l	BB_t	BB_l	BB_t	BB_l
PV1	0.067	0.185	0.168	0.460 ^{ab}	0.578	0.967
PV2	0.100	0.217	0.167	0.517 ^{ab}	0.650	0.983
PV3	0.167	0.350	0.267	0.683 ^{a}	0.634	1.000
PV4	0.167	0.383	0.250	0.667 ^{a}	0.700	0.917
PV5	0.042	0.104	0.042	0.148 ^{c}	0.596	0.979
PV7	0.042	0.183	0.083	0.400 ^{b}	0.604	1.000
PV8	0.167	0.167	0.250	0.542 ^{a}	0.583	1.000
PV9	0.067	0.150	0.150	0.483 ^{ab}	0.667	0.958
PV10	0.050	0.167	0.100	0.367 ^{bc}	0.533	1.000
PV11	0.069	0.169	0.206	0.493 ^{ab}	0.666	0.983
PV12	0.177	0.233	0.149	0.399 ^{b}	0.505	0.932

means with the same letter or no letter in the same column are not significantly different at the 95 % level.

Table 4.5: Heights (cm) at the End of the 1st Year and Beginning of the 2nd Year of Seedlings from Blocks 1 and 2 (n = number of seedlings)

	11/4/89 (before thinning)	(n)	11/4/89 (after thinning)	(n)	5/9/89	(n)
PV1	18.1 a	50	19.2 a	28	19.8 a	28
PV2	15.3 bc	49	15.5 b	30	16.2 b	30
PV3	15.9 abc	49	15.9 b	30	16.4 ab	30
PV4	17.3 ab	46	17.6 ab	30	18.4 ab	30
PV5	15.4 bc	39	16.5 ab	23	17.2 ab	23
PV7	17.7 a	13	17.6 ab	11	18.1 ab	11
PV8	15.6 bc	18	16.8 ab	12	17.7 ab	12
PV9	17.1 abc	49	17.4 ab	30	17.9 ab	30
PV10	17.2 abc	50	18.3 ab	30	18.8 ab	30
PV11	14.9 c	49	15.7 b	29	16.1 b	29
PV12	17.4 ab	24	17.3 ab	18	19.0 ab	18

means with the same letter in the same column are not significantly different at the 95 % level.

Table 4.6: Mean Second Year Height

Height:	Raw (cm)	Log_e (Raw)	Mean Adjusted (cm)
PV1	74.355 a	4.2745 a	71.018 ab
PV2	70.817 a	4.2442 a	70.700 ab
PV3	67.882 a	4.1738 a	65.783 ab
PV4	78.449 a	4.3354 a	76.038 a
PV5	66.585 a	4.1675 a	64.619 b
PV7	68.417 a	4.1562 a	66.167 ab
PV8	72.000 a	4.2417 a	71.917 ab
PV9	67.990 a	4.1921 a	66.948 ab
PV10	67.926 a	4.2092 a	66.652 ab
PV11	67.644 a	4.1720 a	63.142 b
PV12	71.663 a	4.2250 a	69.116 ab

means with the same letter in the same column are not significantly different at the 95 % level.

Table 4.7: Probability (Pr > F) Values For Measured Variables in Tables 4.5 and 4.7

Source:	BK	PV
Raw height	0.0001	0.4639
Log_e (height)	0.0004	0.5660
Mean Adjusted	0.0022	0.6353
FD week 9	0.0003	0.5210
BSweek 35	0.0005	0.0095
FDweek 35	0.0004	0.0146
FDweek 50	0.0124	0.0054

Table 4.8: Proportion of Terminal Bud Set (BS) and Frost Damage (FD)

	FDweek 9	BSweek 35	FDweek 35	FDweek 50
PV1	0.150 a	0.612 bcd	0.355 abcd	0.575 abc
PV2	0.117 a	0.603 bcd	0.397 abc	0.627 ab
PV3	0.217 a	0.500 cd	0.467 ab	0.700 a
PV4	0.183 a	0.683 abcd	0.250 bcd	0.467 abcd
PV5	0.083 a	0.894 a	0.106 d	0.148 d
PV7	0.042 a	0.783 ab	0.217 bcd	0.350 bcd
PV8	0.083 a	0.791 ab	0.208 bcd	0.250 cd
PV9	0.117 a	0.733 abc	0.267 bcd	0.383 abcd
PV10	0.017 a	0.850 ab	0.150 cd	0.200 d
PV11	0.150 a	0.449 d	0.550 a	0.602 ab
PV12	0.194 a	0.660 abcd	0.340 abcd	0.545 abc

means with the same letter in the same column are not significantly different at the 95 % level.

SEE ERRATA

Table 4.8: Correlation Coefficients (r) and Significance (p) of Height, Bud Set and Frost Damage With Climate Variables

	Height		BS_{week35}		FD_{week35}		FD_{week50}	
	r	p	r	p	r	p	r	p
LAT	0.010	0.9467	0.473	0.0012	-0.344	0.0221	-0.468	0.0014
LON	0.015	0.9240	0.063	0.6849	-0.056	0.7198	-0.014	0.9273
ALT	0.066	0.6717	0.009	0.9825	-0.028	0.8580	-0.038	0.8052
MAT	0.066	0.6725	-0.539	0.0002	0.424	0.0042	0.550	0.0001
MCT	0.069	0.6554	-0.518	0.0003	0.379	0.0111	0.519	0.0003
MWT	0.016	0.4145	0.158	0.3053	0.200	0.1929	0.238	0.1196
TSM	0.009	0.9522	-0.508	0.0004	0.409	0.0059	0.539	0.0002
MAR	0.008	0.9594	-0.387	0.0095	0.262	0.0863	0.408	0.0059
MAS	0.011	0.9461	0.322	0.0332	-0.248	0.1050	-0.294	0.0525
FFD	0.012	0.9401	-0.364	0.0151	0.254	0.0956	0.347	0.0210
BS_{week35}	0.064	0.6810						
FD_{week35}	0.008	0.9604	-0.924	0.0001				
FD_{week50}	0.032	0.8355	-0.850	0.0001	0.899	0.0001		

n.b. See section 2.2 for definitions of climate variables

Figure 4.1: Germination Values of PV's By Temperature

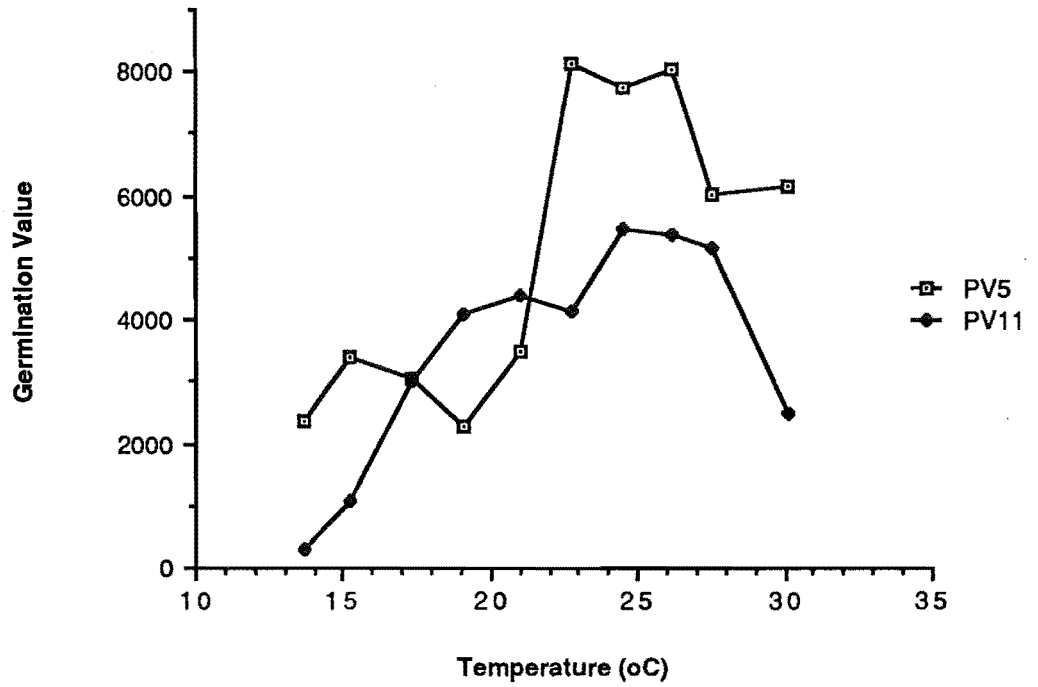


Figure 4.2: PV11 Percent Germination By Temperature

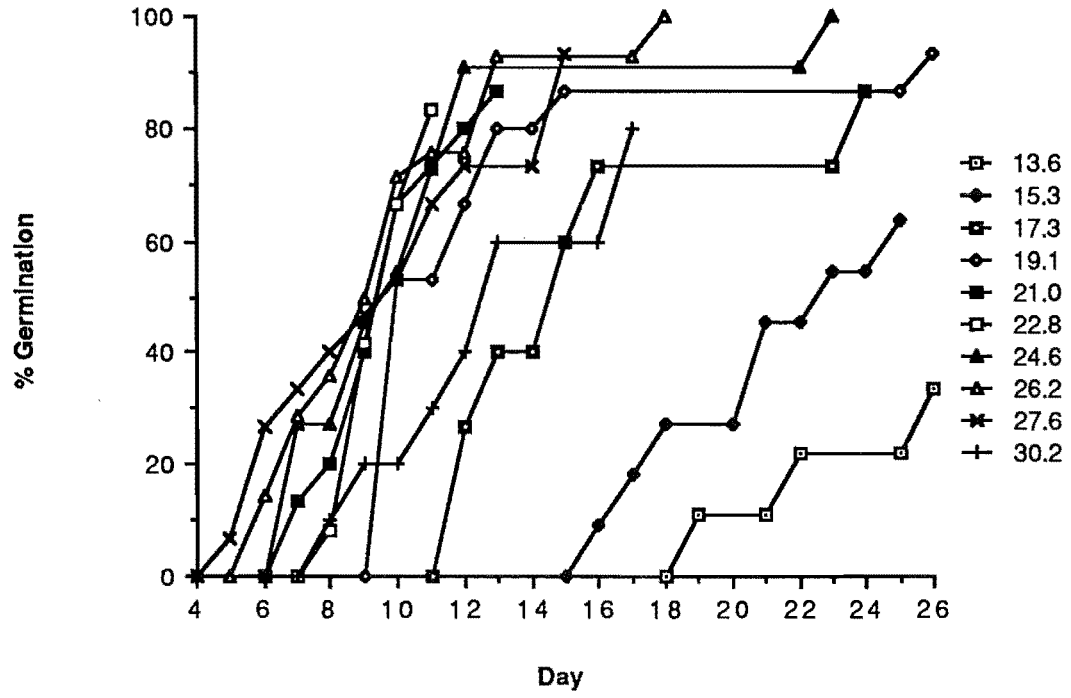


Figure 4.3: Germination Curves For PV5 (3 Best GV's)

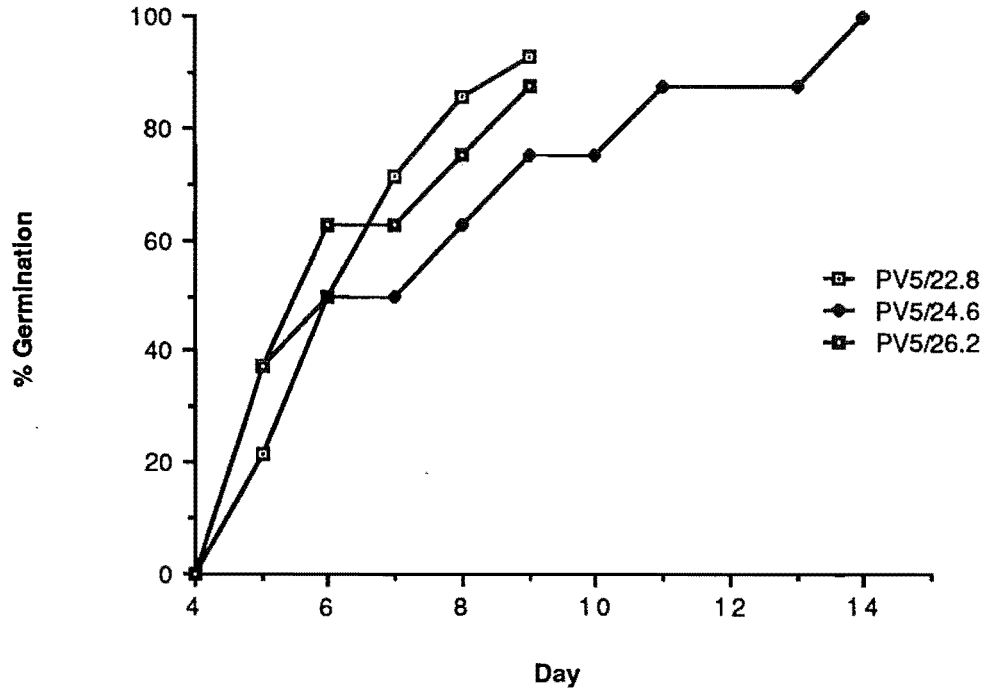


Figure 4.4: Germination Curves For PV11 (3 Best GV's)

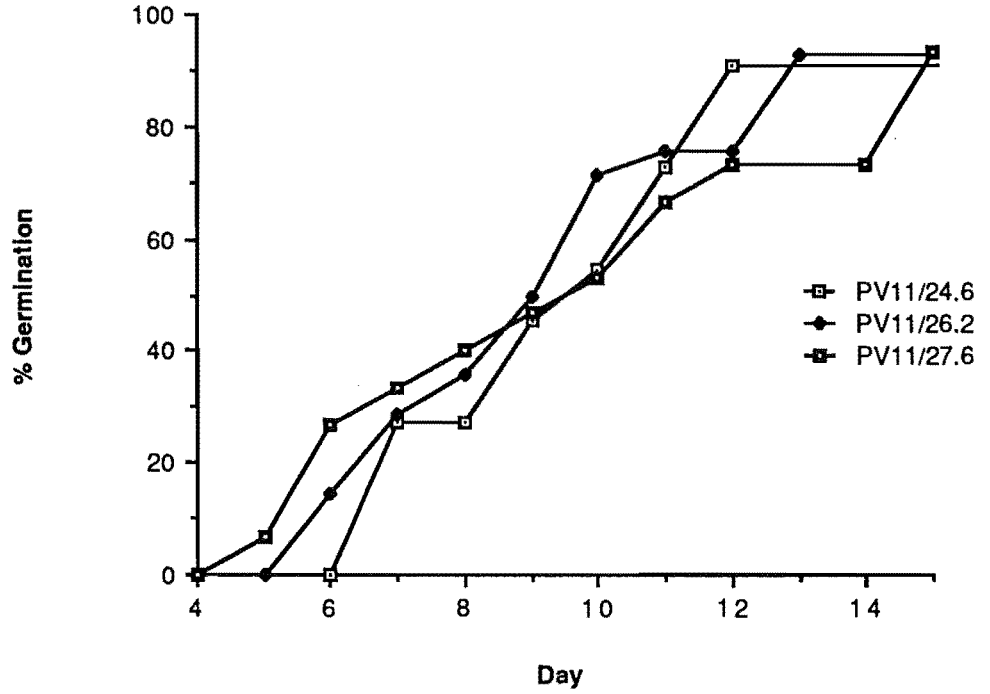


Figure 4.5: Nursery Layout of Provenances

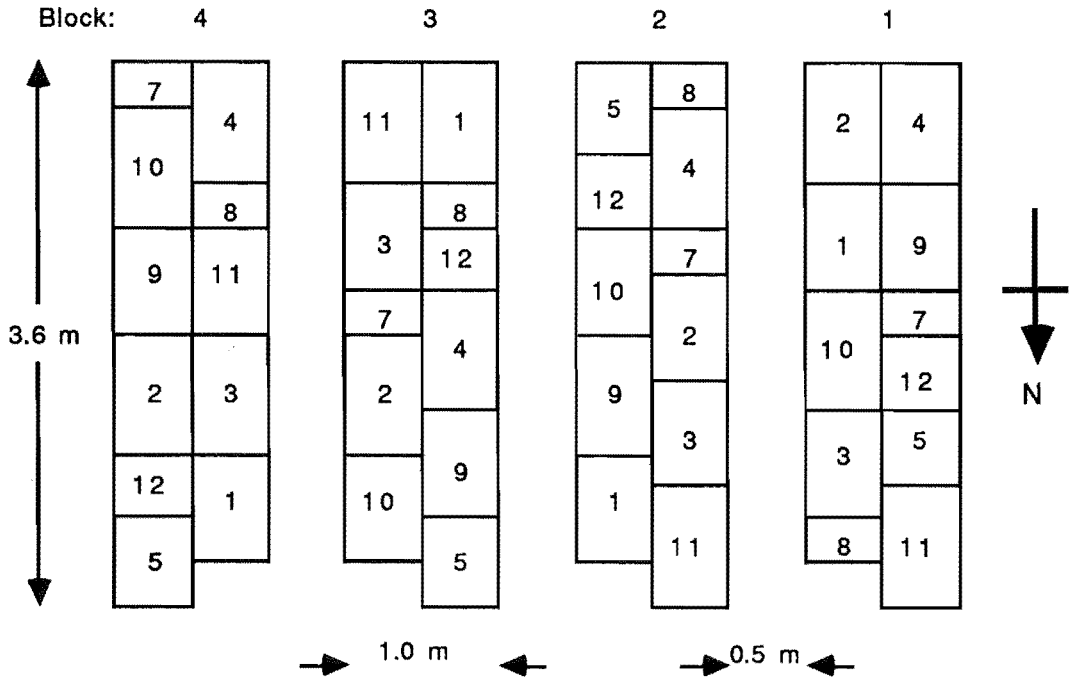


Figure 4.6: Terminal and Lateral Bud Burst (All PV's)

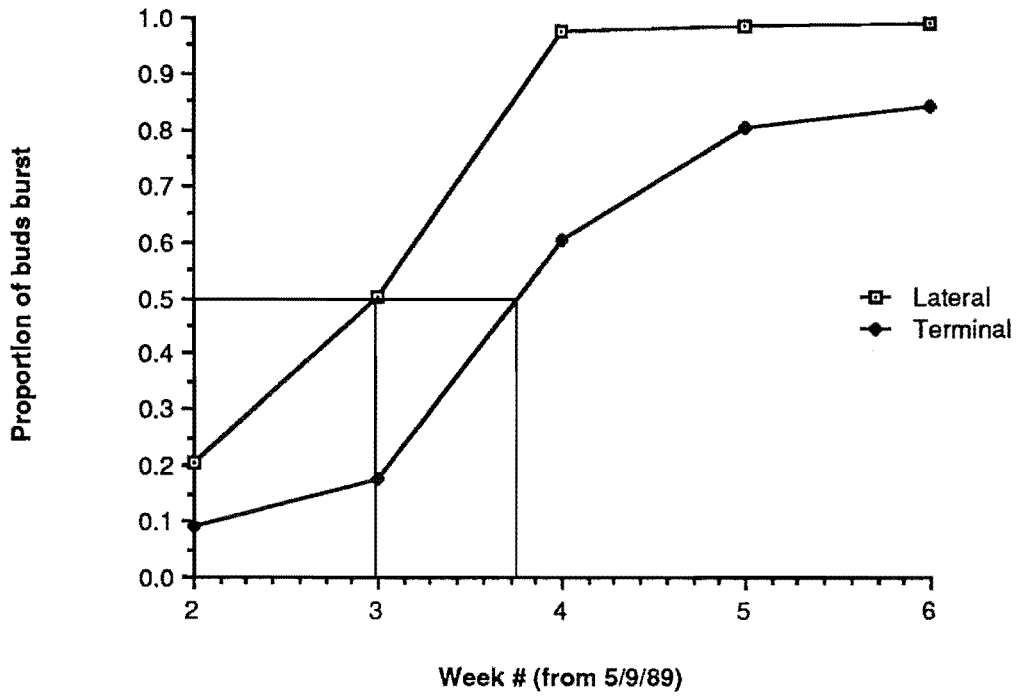


Figure 4.7: Second Year Height Growth

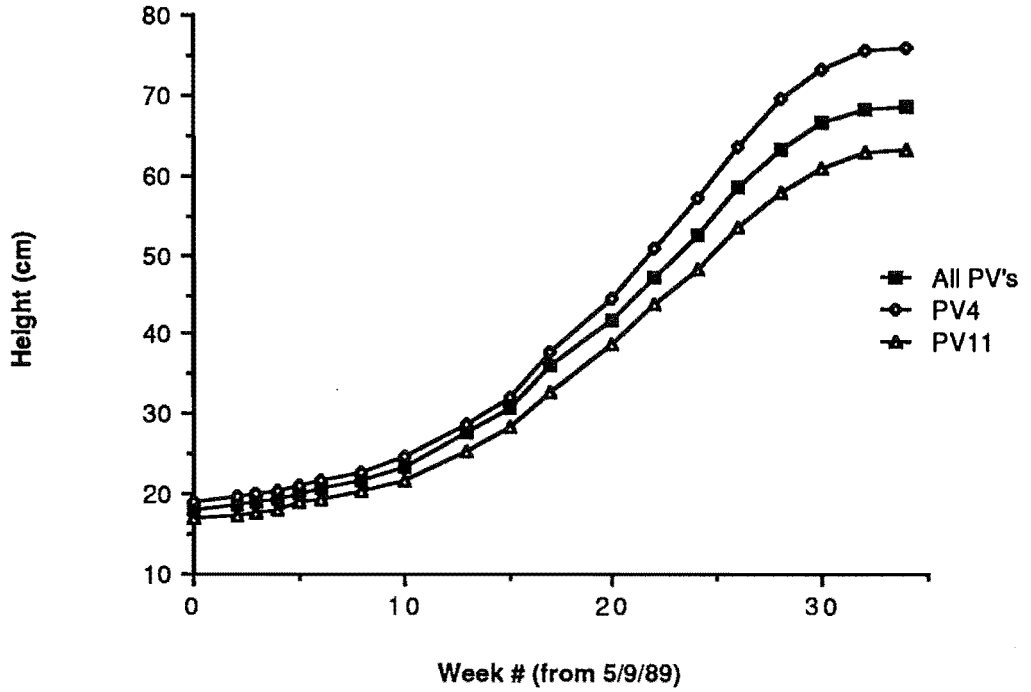


Figure 4.8: Terminal and Lateral Bud Set (All PV's)

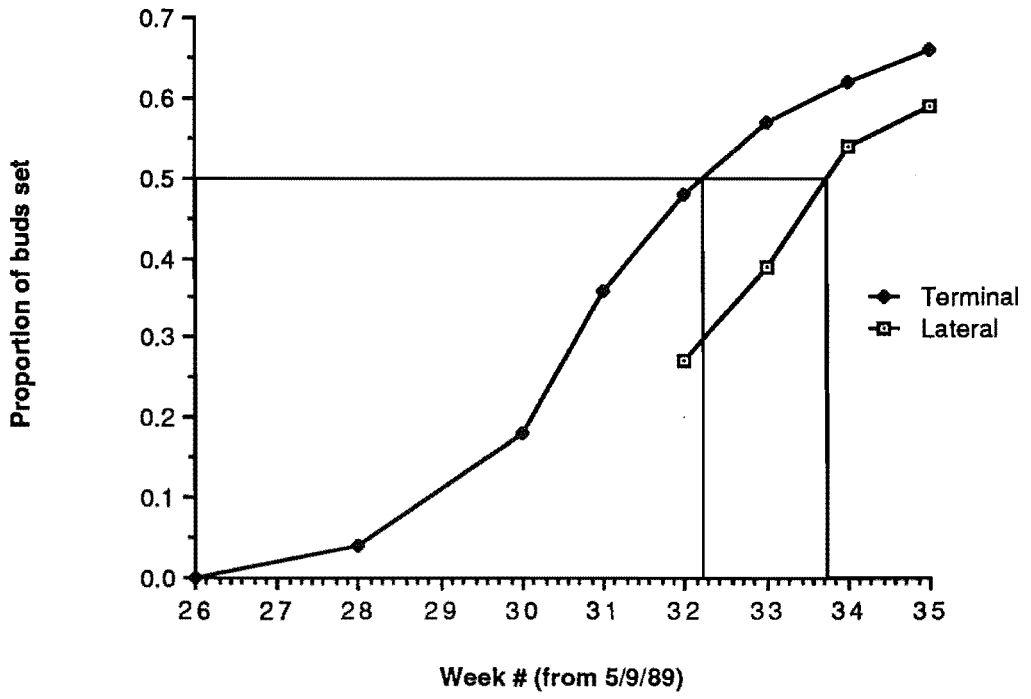


Figure 4.9: Bud Set (BS) and Frost Damage (FD) at Week 35

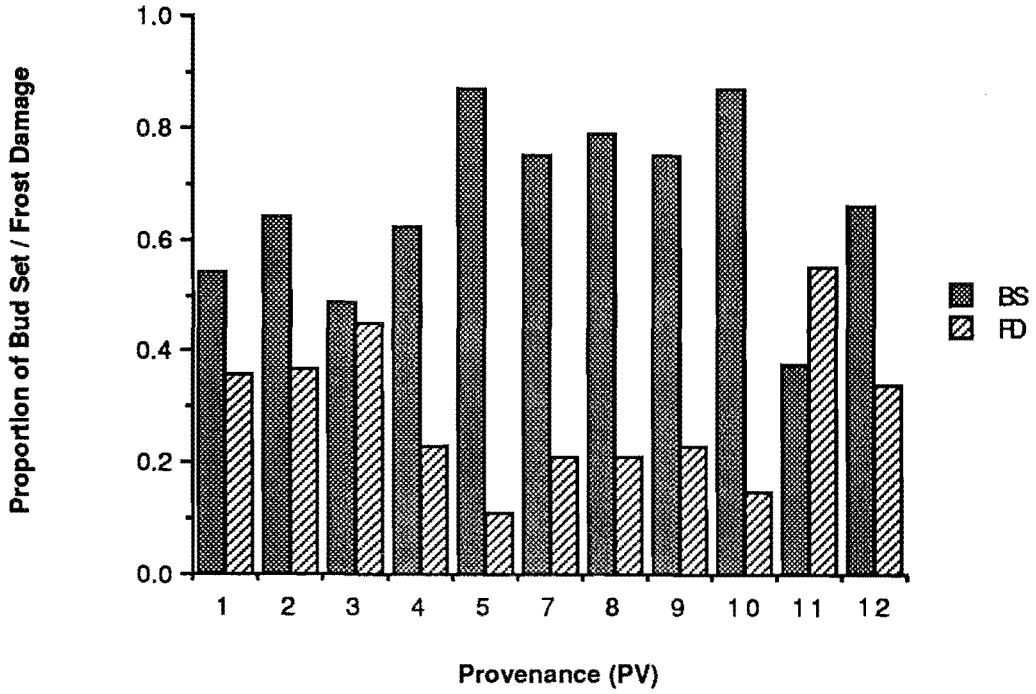


Figure 4.10: Frost Damage by Provenances at Weeks 35 and 50

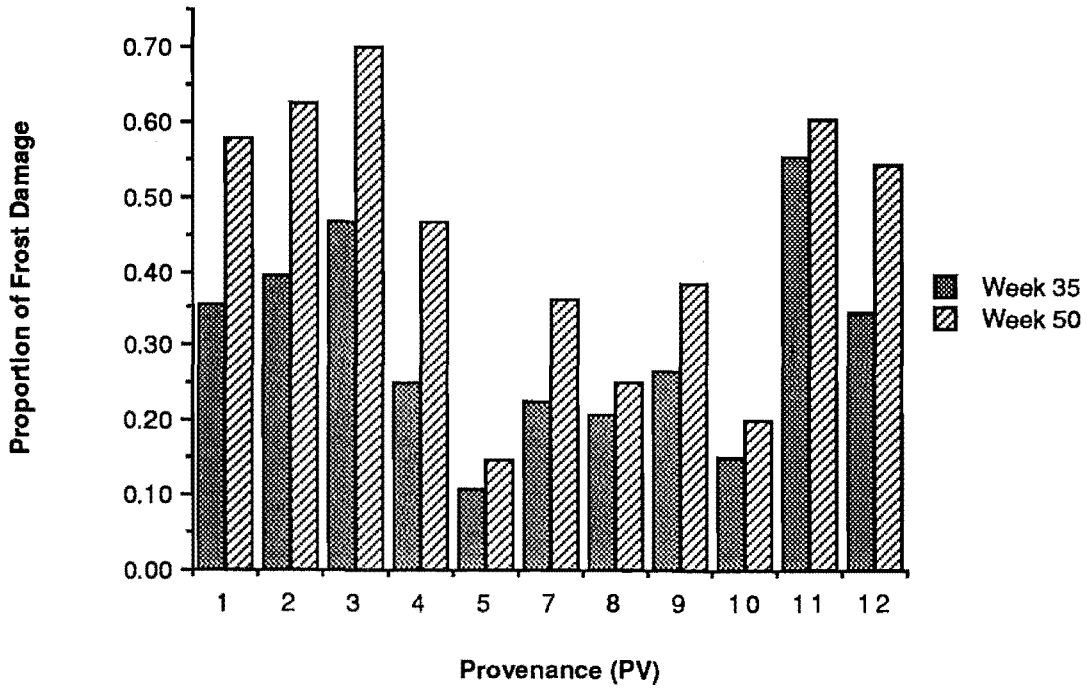


Plate 4.1: Second Year Height Growth, Midway Through the Growing Season (Block 1 in foreground)

Plate 4.2: Frost Damage (Blocks 3 and 4) After The Second Growing Season (Week 50)

CHAPTER V

GENETIC VARIATION IN EIGHT PROVENANCES

1. INTRODUCTION

Genetic variation between provenances has usually been assessed by way of morphological traits (growth rate, disease resistance, frost tolerance *etc.*). While this directly measures economically important traits, environmental influences can confound the observed response (phenotype). In order to minimise environmental effects it has been necessary to conduct provenance trials where different provenances are grown on the same site (Hamrick, 1989), frequently using several to many sites. Because morphological characteristics are usually controlled by several genes, specific genetic information is not readily obtainable through provenance trials (Rothe, 1991).

Isozyme analysis is an alternative method for examining genetic variation. Isozymes are the direct product of specific allelic genes (Rothe, 1991); they are therefore considered as reliable gene markers and have several advantages over the study of morphological traits: Discrete Mendelian inheritance; codominance enabling allele frequencies to be calculated directly; estimation of levels and distribution of genetic variation can be compared directly between provenances (Hamrick, 1989).

Different enzymes and variants of those enzymes have differing protein structures and thus have differing net electrical charges. Isozymes (iso-enzymes) are enzymes that share a common substrate but differ in electrophoretic mobility and are revealed under electrophoresis of tissue extracts of plants in starch gels (Wendel and Weeden, 1989). An electrical current applied to the starch gel forces the enzymes to migrate through the gel and the extent of migration of the isozyme depends upon its electrical charge. Following electrophoresis the gel is sectioned and each section is stained for specific enzyme systems. A more detailed account of starch gel electrophoresis is given in Wendel and Weeden (1989).

As an extension to the more usual field trial approach (see chapter IV) isozyme analysis using starch gel electrophoresis was carried out on the *C. lanceolata* provenances used in this study.

2. MATERIALS AND METHODS

Seed from eleven provenances were placed on moist filter paper in petri dishes and left to germinate. Upon germination and when approximately 5 mm of root radicle had emerged from the seed, embryonic tissue was removed from the endosperm and individually homogenised in 0.5 ml cups with aspen extraction buffer (see appendix D for recipe). Four paper wicks were placed in each homogenised solution and the cups were then placed in a freezer until required for electrophoresis.

2.1 Provenance Material

Uneven germination of provenances meant that only eight provenances could be used in the resulting isozyme analysis. The eight provenances used in electrophoresis were: PV's 1 - 5, 9 - 11. See appendix A for full details. Twenty seeds were used per provenance except for PV9 where only 13 seeds were available.

2.2 Electrophoresis

Prior to electrophoresis the homogenised tissue was removed from the freezer and allowed to thaw. One wick from each cup was placed in 11.5 % w/v starch gels. Wicks soaked in homogenised pea tissue (standard) were placed between every 10 wicks of *C. lanceolata* tissue; wicks soaked in red food dye were placed at either end of the gels as end markers.

Gels were then placed on buffer bridges and an electric current of 35 mA was applied for 30 minutes after which the paper wicks were removed, the gels covered with plastic and ice pads and the electric current was re-applied at 50 mA for another 4 - 5 hours.

When electrophoresis was completed the gels were removed and horizontally sliced into eight 1 mm thick slices. The strips were then placed in trays and stained for a specific enzyme system. Enzymes stained for were:

Gel type	Enzyme
Histadine	ADH, APH, DIA, G6PDH, IDH, MDH, ME, 6PG, PGM
Poulik	AAT, ACON, EST, MR, PER, PGI, SOD

For full names of the enzyme systems and gel recipes see appendix D.

2.3 Analysis

In most enzyme systems only two alleles were present and so were labelled as fast (F) or slow (S) alleles, a third allele was present in PGI-1 and was labelled very slow (VS). As

individual embryo (diploid) tissue was used allele frequencies for each enzyme system were calculated. Alleles were homozygous if there was only one form (F, S, or VS) present per sample and heterozygous if more than one form could be seen per sample. Results were analysed using the BIOSYS-1.7 computer program (Swofford and Selander, 1989).

Genetic variation measures for each provenance calculated were: Nei's (1978) unbiased estimate of heterozygosity (H); Mean number of alleles per locus (A); percentage of polymorphic loci (P) where the frequency of the most common allele is ≤ 0.95. Genetic variation between provenances was measured by: Nei's (1978) unbiased genetic distance (D) and unbiased genetic identity (I). Cluster analysis by unweighted pair group method was then used on D to construct a phylogenetic tree.

Total genetic diversity of the species (H_t) is comprised of within population and between population components (H_S and D_{St} respectively). Partitioning of these components is measured by Nei's (1973) relative measure of differentiation (G_{St}) where:

$$G_{St} = D_{St}/H_t$$

G_{St} is therefore a measure of total genetic diversity attributable to differences between populations. G_{St} values for each polymorphic locus and for the species as a whole were calculated.

3. RESULTS

3.1 Allelic Frequencies and Genetic Variation Within Provenances

A total of 14 loci from 10 enzyme systems showed activity and were able to be successfully scored. The allelic frequencies and heterozygosity for each locus (*H*) are given below in Table 5.1. Six enzyme systems failed to produce any result (ADH, APH, MDH, ME, ACON, PER), either due to inactivity or technical problems. The first locus of DIA (DIA-1) was too blurred to score effectively.

Variable loci other than IDH generally had *H* 's of 40-50 %. The exceptions were PV10 and PV11 which had higher frequencies of one allele over another compared with other provenances, and resulting lower *H* values (*e.g.* PV10 in AAT-1 and PGI-1, PV11 in PGI-1.

Results of interest were seen in PGI-1 and IDH loci. PGI-1 had three alleles present in four provenances. The third allele was designated very slow (VS) and was always homozygous in form, frequency was low. The heterozygous form of IDH showed dimerism (an intermediate "allele" occurring between the fast and slow alleles, but not seen in the homozygous forms). However this locus was generally not very variable.

Mean expected heterozygosity (H) for each provenance is given in Table 5.2. Results show that while H ranges from 0.069 to 0.126, large standard errors indicate that there is little difference between provenances.

Mean number of alleles per locus and percentage of polymorphic loci are also given in Table 5.2. A values are similar ranging from 1.2 to 1.4 indicating uniformity of the provenances. This is further shown in P values which are either 21.4 % (in three provenances) or 28.6 %.

3.2 Genetic Variation Between Provenances

Nei's (1978) unbiased genetic distance (D) and unbiased genetic identity (I) are given in Table 5.3. For I a value of one means that the provenances have identical frequencies of alleles, a zero value indicates that there are no alleles in common. D is a measure of genetic differentiation among provenances. From the table it is clear that D and I are negatively correlated as for each comparison between provenances $D = -\log_e(I)$. As I values are either one or close to one (and conversely D values are close to zero) there is little genetic variation between provenances in terms of allele frequencies.

Nei's (1973) relative measure of differentiation (G_{st}) values for each polymorphic locus and for the species as a whole are shown in Table 5.4. Genetic differentiation was low, varying between 0.5 % ($G_{st} = 0.005$) for AAT-2 and 8.4 % ($G_{st} = 0.084$) for PGI-1. Overall differentiation between provenances was low at 4.4 % ($G_{st} = 0.044$) indicating that most of the genetic variation occurred within, rather than between provenances.

A cluster diagram of D (Figure 5.1) shows that most provenances are closely clustered although PV10 and PV11 diverge from the group earlier. It would appear that provenances in general are closely related (genetically similar).

4. DISCUSSION

4.1 Variation Between Provenances

The proportion of genetic diversity attributable to differences between provenances was 4.4 % ($G_{st} = 0.044$), thus 95.6 % of variation occurs within provenances. Similar (low) G_{st} values have been reported for wind pollinated conifers (0.068) in Brown and Moran (1981), and wind pollinated plants in general average 6 % of variation between populations (Levin, 1986).

Genetic diversity within populations appears to be high in most conifers, regardless of the scale of geographic distribution. For species with small scale or restricted ranges; 96.4 % of total genetic diversity was contained within populations of *Taxodium distichum* (Liu *et al.*, 1990), more than 99 % was found in *Abies fraseri* (Diebel and Feret, 1991), and

95.8 % (G_{st} = 0.042) was found in *Picea abies* populations in Italy (Giannini *et al.*, 1991). Billington and Sweet (in press) found low levels of variation between populations; 2.2 % for *Dacrydium cupressinum* and 5.6 % for *Dacrycarpus dacrydioides*, values which were similar to those of Hawkins' (1989) of 3.2 % and 6.75 %.

In other conifers with wider distributions, low levels of variation between populations are also reported, for example: 1 - 1.8 % for *Pseudotsuga menziesii* in breeding zones and sites in southwestern Oregon (Merkle and Adams, 1987; Morgan and Adams, 1989) and 6.6 % for altitudinal zones (Billington *et al.*, in press); and between 2 - 8 % for several *Pinus spp.* in Hawkins (1989). *Thuja occidentalis* had 96.9 % of total genetic diversity within stands (Matthes-Sears *et al.*, 1991).

Higher levels of variation between populations are often attributed to a species which has a restricted range and/or disjunct populations where gene flow is reduced allowing differences to evolve, *e.g. Sequoiadendron* had 10 % of variation between populations (Fins and Libby, 1982). However the range of *C. lanceolata* is not restricted in this sense and morphological provenance differences are slight (see chapter IV). *C. lanceolata*, then appears to behave in a similar manner to most conifers with wide geographical ranges.

Genetic distances (D) also show that there is little differentiation between provenances as most distances are close to or equal to zero. This is clearly shown in the cluster diagram based on D. The divergence of two provenances (PV10, PV11) from the rest does not appear to follow any (geographical) trend (latitude, longitude, altitude); the divergence may in fact be of no significance in terms of provenance variability as stand and collection details are unknown.

For PV11 at least, seed was collected from the "green" strain as opposed to the "blue" strain (PV12 at the same site, but not tested here). A selective collection would tend to reduce variability and this is seen to a degree in Table 5.2 where PV11 has the lowest A, P, and H. The difference then is probably not a "true" provenance difference and of little genetic value (as gene flow between strains on the same site would not be restricted). Given the long history of cultivation of *C. lanceolata* it is likely that seed transfer between regions would have occurred. This, as well as the conifer mating system, would serve to reduce variability between populations.

Other studies with *C. lanceolata* have suggested that provenance/seed source differences exist. Huang *et al.* (1986) identified 7 types of esterase patterns from 63 seed sources. There was less variation in (geographical) centres of each pattern but this increased further away from the centres. West and southwest areas of Sichuan and south west Yunnan were centres of polymorphism and were suggested as possible origins of *C. lanceolata*. Yu and Zhang (1986) showed provenance differences in 11 provenances (including PV2/11, PV9, and PV8 in this study). However the differences were not

related to latitude. Interestingly in the above studies EST zymograms showed polymorphism, but in this experiment EST was monomorphic only. Although differences were stated the lack of any genetic measure of variability or statistics precludes a comparison with the results obtained here.

Fu (1987) reported on variation in populations in Sichuan. There was a variation trend in north - south regions with southern regions having higher activity and more bands. Similarly Müller-Starck and Liu (1989a) showed significant differences between two Sichuan provenances; but experiment conditions differed as noted above. Such differences may be real but small relative to the total variation within the species as a whole, as is the case in this study.

This does not necessarily imply that there are no provenance differences in this study; enzyme systems that were tested may be neutral to any selection pressure that operates on the species. Merkle and Adams (1987), for example, found little genetic diversity attributable to breeding zones and a lack of geographic or environmental pattern in allelic variation for *Pseudotsuga menziesii* although geographic variation is evident in quantitative traits. Similarly Moran and Adams (1989) found that while there was considerable genetic variation present in stands of *Pseudotsuga menziesii*, there was no significant difference between stands even though marked variation in seedling characters had been found previously. While other quantitative differences may exist between populations, most studies demonstrate that isozymes are not traits subjected to intense selection pressures (Diebel and Feret, 1991). In Diebel and Feret's study allele and genotype frequencies were not correlated with any environment characters. For *C. lanceolata* differences may have been seen using other enzyme systems, and there may well be regional variation in Chinese populations of *C. lanceolata.* However the absence of pronounced differences in either morphological or physiological characters in this and other experiments suggests that there is little genetic difference between the study provenances.

4.2 Species Genetic Variability

Results should be considered preliminary due to lack of details of the seed collections, stand histories, and sample sizes. Nevertheless there is a consistent pattern of low genetic variability for the species as a whole.

For *C. lanceolata* mean number of alleles per locus is 1.33 (Table 5.2), this compares to an average of 2.12 for gymnosperms (Hamrick *et al.*, 1979) and 2.29 for conifers (Hamrick *et al.*, 1981). More alleles per locus have been reported for *Pseudotsuga menziesii*; 2.46, 2.30 and 1.6 (Merkle and Adams, 1987; Moran and Adams, 1989; and Billington *et al.*, in press respectively); and 1.45 - 1.83 for *Podocarpus spp., Phyllocladus alpinus, Lagarostrobus colensoi, Lepidothamnus intermedius* (Billington

and Sweet, in press). An isolated relic population of *Abies fraseri* had 1.10 (Diebel and Feret, 1991) while disjunct populations of Italian *Picea abies* had 1.667 - 2.048 (Giannini *et al.*, 1991). Other conifers reported in Diebel and Feret (1991) are similarly higher: *Picea abies*, 1.65 -1.75; *Pinus aristata*; 1.49; and *Picea marianna*, 1.24 - 1.38. *C. lanceolata* then, appears to have a comparatively low mean number of alleles per locus, similar to that of some New Zealand podocarps (*e.g.* Billington and Sweet, in press; Hawkins, 1989), *Abies fraseri* and *Picea marianna.*

Percentage of polymorphic loci (25.9 %) is similarly low in comparison to conifers in general (67.7 %, Hamrick *et al.*, 1981) and the species listed above by Billington and Sweet (in press) but is close to that of *Dacrydium cupressinum* and *Dacrycarpus dacrydioides* (Hawkins, 1989) and other podocarps (Billington and Sweet, in press). *Abies fraseri* is also low at 30.8 % (Diebel and Feret, 1991). In *Pseudotsuga menziesii* very high percentages of 47.4 % (Billington *et al.*, in press) and 70.1 - 71.7 % (Morgan and Adams, 1989; Merkle and Adams, 1987) have been reported, *Picea abies* had a percentage of 45.5 % (Giannini *et al.*, 1991). Only a few studies have been reported for other *Taxodiaceae* (Müller-Starck and Liu, 1988); *Sequoiadendron* had 50 % polymorphic loci (Fins and Libby, 1982). Low polymorphism has been reported for *Thuja occidentalis*, *T. plicata*, *Pinus resinosa*, and *Larix occidentalis*, all species with large ranges (Matthes-Sears *et al.*, 1991). The overall picture suggests that *C. lanceolata* has considerably lower variation compared with many other conifers.

As with A and P, conifers in general are much more heterozygous (0.207) than *C. lanceolata* (Hamrick *et al.*, 1981). Heterozygosity at 0.108 differs from those reported for embryo tissue of two provenances of *C. lanceolata* from Sichuan (not represented in this study) by Müller-Starck and Liu (1989a); these were considerably higher at 0.322 and 0.275. Different enzyme systems and larger seed samples were used in that study, the enzyme systems were all polymorphic which would account for greater heterozygosity. *Sequoiadendron* had an expected mean heterozygosity of 0.140 (Finns and Libby, 1982), while *Picea abies* had 0.165 (Giannini *et al.*, 1991). Results are comparable to *Podocarpus spp.* but greater than other podocarp species in Billington and Sweet (in press). *Pseudotsuga menziesii* heterozygosities are either similar (0.109 in Billington *et al.*, in press) or greater (0.178 in Merkle and Adams, 1987; 0.164 in Moran and Adams, 1989). Interestingly measures of genetic variability in Merkle and Adams (1987) are consistently higher than in Billington *et al.* (in press), due to use of megagametophyte tissue rather than embryo tissue, and different enzyme systems. Thus the lower H value for *C. lanceolata* in this study is not necessarily invalidated by those of Müller-Starck and Liu (1989a).

Low variability has been reported in New Zealand podocarps (Hawkins, 1989), as well as *Pinus resinosa* (Fowler and Morris, 1977), *P. torreyana* (Ledig and Conkle, 1983),

Abies fraseri, (Diebel and Feret, 1991), *Thuja plicata* (Copes, 1981), and *T. occidentalis* (Matthes-Sears *et al.*, 1991). *C. lanceolata* also appears to fall within this group.

A number of factors cause low variability. Conifer species in general are considered to have high levels of genetic variation (Hamrick *et al.*, 1981; Mitton, 1983), due to such factors as longevity, wind pollination and out-crossing (Mitton, 1983), a high degree of inbreeding depression is evident (Yazdini *et al.*, 1985). Seed samples may therefore contain a high degree of "selfed" seeds. In a 100 year old stand of *Pinus sylvestris* the genetic structure of adult trees was close to Hardy-Weinberg equilibrium, while seed samples deviated significantly from this pattern (Yazdini *et al.*, 1985). Inbreeding (surplus of homozygotes) was the cause for this deviation and was eliminated before trees were 10 - 20 years old. Similarly isozyme analysis of *Sequoiadendron* showed that the level of heterozygosity in embryo tissue was lower than that in mature tissue, suggesting inbreeding was occurring (Finns and Libby, 1982). An examination of the reproductive system of *C. lanceolata* also indicated that inbreeding was the most prominent component (Müller-Starck and Liu, 1989b).

"Evolution bottlenecks" arising from reduced population size in the species' past (with corresponding genetic drift) can also serve to reduce variability (Ledig and Conkle, 1983). Bottleneck causes have been suggested for a number of conifer species with low variability, *e.g. Abies fraseri* (Diebel and Feret, 1991), *Thuja occidentalis* (Matthes-Sears *et al.*, 1991), *Sequoiadendron* (Finns and Libby, 1982). For these species, as well as *Thuja plicata*, *Pinus resinosa*, and *Larix occidentalis* (reported in Matthes-Sears *et al.*, 1991), bottlenecks arose from glaciation reducing population distribution and size, creating (more) uniformity. The subsequent time to present and/or expansion of the species has not been sufficient to allow differentiation to become apparent.

The present day geographic distribution of *C. lanceolata* occurs over a wide range of altitudes and area (see Introduction). *Cunninghamia* has an evolutionary history extending back to the Tertiary period (25 - 65 million years before present). Its present day distribution in central-southern China contrasts with fossil remains from the Tertiary in Japan (Sakai, 1971; Tanai, 1972; Liu, 1966) and northern China (Liu, 1966). *Cunninghamia* as part of the flora of Taiwan has close phytogeographical affinity to North America (Liu, 1966) and fossil records in the Pacific northwest region of America date back to the Miocene and Oligocene epochs of the Tertiary period as reported in Miller (1990). *Cunninghamiostrobus geodertii*, a likely ancestor of *Cunninghamia* was present in western North America in the early Oligocene (Miller and Crabtree, 1989; Miller, 1990). Other fossils of *Cunninghamiostrobus spp.* date back to the early Cretaceous period in California and the late Cretaceous in Japan (Miller and Crabtree, 1989).

During the Tertiary period the climate was generally mild and was characterised by large temperate hardwood forests (Arcto-Tertiary flora) throughout much of the present day

boreal zone (Pielou, 1979; Neill, 1970). The Berring connection, a land bridge between North America and Eurasia, existed at various times during the Tertiary and provided a corridor for exchange of floral species between the two land masses (Pielou, 1979; Cox and Moore, 1985). Evidence of exchange can be seen in disjunct evolutionary relicts such as *Magnolia* and *Liriodendron* which occur in both North America and China (and south east Asia) but nowhere else (Cox and Moore, 1985). Cooling of temperature in the late Tertiary brought about a replacement of the Arcto-Tertiary flora with boreal forest at high latitudes (Pielou, 1979) and a reduction in area occupied by megathermal plants (in this Arcto-Tertiary group) leading to restricted ranges (Cox and Moore,1985). Subsequent glaciation during the Quaternary while not extending fully to southern China and south east Asia, nevertheless, exerted an influence on climates there (Neill, 1970; Pielou, 1979). Glaciation led to the present day restricted ranges of the Arcto-Tertiary relict species now concentrated in China and Japan (Neill, 1970; Sakai, 1971); refugia were mostly in the eastern portion of Eurasia (China and Japan) as this area offered large and easy access (Neill, 1970). From other isozyme studies which suggest that *C. lanceolata* may have spread from centres in Sichuan and Yunnan (Huang *et al.*, 1986) it is possible that the cooling temperatures during the Tertiary could have caused the species to "retreat" to these centres and from there spread out again to its present distribution.

However both the extent of it's geographic area and long history of cultivation suggests that this refugia concept may not necessarily account for low variability. Similarly climate stability would probably not have accounted for low variability as it is suggested for oceanic climate species (Hawkins, 1989). Continental climate changes were more pronounced with successive ice ages (Cox and Moore, 1985). A long history of cultivation may serve to reduce variability between populations by seed exchange between areas; furthermore selection within populations for particular traits (*e.g.* fast growth) over a long period would also reduce variability.

5. SUMMARY

The overall picture of genetic variation for *C. lanceolata* from this study indicates that the species has a low level compared with other conifer species. Levels are comparable to those of New Zealand podocarps, *Abies fraseri*, and *Thuja occidentalis*, but below the average of conifers in general. However while low variability for these species has been attributed to climate stability and/or evolutionary bottlenecks, the more probable cause for *C. lanceolata* is inbreeding.

Variation between provenances is also low but this is similar to most conifer species with an unrestricted range or non-disjunct populations. As seed collection and stand details are unknown this low inter provenance variation does not necessarily indicate that provenance differences are not real. Although this experiment indicates that these seed sources are very similar (genetically), at least for the enzyme systems tested, other studies

have reported provenance differences. Thus there may be real differences in truly representative, separated populations.

In this study the lack of population differentiation is also evident in other quantitative measures (morphological and physiological). It would therefore appear that these provenances are of low variability genetically, possibly due to the species' long history of cultivation and seed transfers.

Table 5.1: Allelic Frequencies and Heterozygosity (*H*) of 14 Enzyme Loci For 8 Chinese fir Provenances

Locus	Allele	PV1	PV2	PV3	PV4	PV5	PV9	PV10	PV11
AAT-1	F	0.275	0.375	0.475	0.350	0.375	0.423	0.150	0.225
	S	0.725	0.625	0.525	0.650	0.625	0.577	0.850	0.775
	(H)	*0.409*	*0.481*	*0.512*	*0.467*	*0.481*	*0.508*	*0.262*	*0.358*
AAT-2	F	0.475	0.400	0.475	0.425	0.425	0.462	0.400	0.500
	S	0.525	0.600	0.525	0.575	0.575	0.538	0.600	0.500
	(H)	*0.512*	*0.492*	*0.512*	*0.501*	*0.501*	*0.517*	*0.492*	*0.513*
AAT-3	F	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
PGI-1	F	0.575	0.575	0.625	0.600	0.550	0.462	0.750	0.950
	S	0.375	0.425	0.325	0.250	0.400	0.538	0.250	0.050
	VS	0.050	0.000	0.050	0.150	0.050	0.000	0.000	0.000
	(H)	*0.540*	*0.501*	*0.514*	*0.569*	*0.549*	*0.517*	*0.385*	*0.097*
PGI-2	F	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
IDH	F	1.00	0.950	0.875	0.975	0.875	0.885	0.925	1.00
	S	0.00	0.050	0.125	0.025	0.125	0.115	0.075	0.00
	(H)	*0.000*	*0.097*	*0.224*	*0.050*	*0.224*	*0.212*	*0.142*	*0.00*
PGM	F	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
MR	F	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
EST-1	F	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
EST-2	F	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
G6PDH	F	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
DIA-2	F	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
6PG-1	F	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
SOD	F	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 5.2: Genetic Variability at 14 Loci

	n	A*	P*	H*	$H_{std\ err}$
PV1	20	1.3	21.4	0.104	0.056
PV2	20	1.3	28.6	0.112	0.055
PV3	20	1.4	28.6	0.126	0.058
PV4	20	1.4	21.4	0.113	0.058
PV5	20	1.4	28.6	0.125	0.058
PV9	13	1.3	28.6	0.125	0.058
PV10	20	1.3	28.6	0.091	0.091
PV11	20	1.2	21.4	0.069	0.043
ALL PV's	19.1	1.33	25.9	0.108	-

* see section 2.3 for definition of symbols

Table 5.3: Nei (1978) Unbiased Distance (top), and Unbiased Identity (bottom)

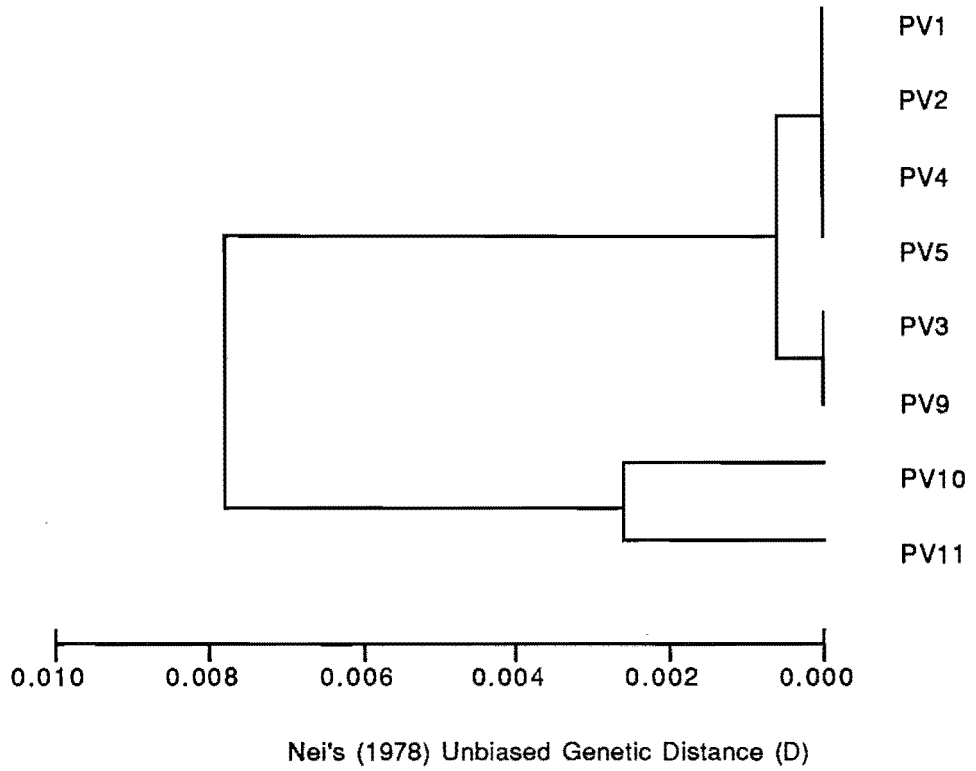
	PV1	PV2	PV3	PV4	PV5	PV9	PV10	PV11
PV1	-----	0.000	0.001	0.000	0.000	0.000	0.001	0.007
PV2	1.000	-----	0.000	0.000	0.000	0.000	0.004	0.011
PV3	0.999	1.000	-----	0.000	0.000	0.000	0.007	0.010
PV4	1.000	1.000	1.000	-----	0.000	0.002	0.002	0.006
PV5	1.000	1.000	1.000	1.000	-----	0.000	0.004	0.012
PV9	1.000	1.000	1.000	0.998	1.000	-----	0.009	0.019
PV10	0.999	0.996	0.993	0.998	0.996	0.991	-----	0.003
PV11	0.993	0.989	0.990	0.994	0.988	0.981	0.997	-----

Table 5.4: Nei's (1973) Genetic Differentiation Between Provenances (G_{st})

Loci	AAT-1	AAT-2	PGI-1	IDH-1	Mean
G_{st}*	0.045	0.005	0.084	0.042	0.044

* see section 2.3 for definition of G_{st}

Figure 5.1: Plot of "Relatedness" of Provenances



CHAPTER VI

GROWTH RESPONSE OF SEEDLINGS FROM SEVERAL PROVENANCES TO DIFFERENT TEMPERATURES

1. INTRODUCTION

Temperature is a key factor in plant growth and one that is especially so early on in seedling development. Temperature affects the rate of physical processes (diffusion and transportation) and metabolic processes in plants (Downs and Hellmers, 1975), such as photosynthesis and respiration which primarily depend on enzymatic reactions. It also strongly influences the balance between photosynthesis and respiration (Bannister, 1976).

The response of plant growth to temperature typically follows an asymmetric bell shaped curve with three features: Minimum and maximum temperatures for plant growth, and the optimum temperature range *i.e.* the range in which highest rates of growth can be maintained (Fitter and Hay, 1981). The optimum range therefore represents temperatures at which the plant's physical and metabolic processes are balanced and enzymatic reactions are optimised.

A large number of studies on tree seedling growth response to temperature have been carried out. Results show a large variety of optimum temperature ranges and temperature conditions, with the latter seeming to fall into three categories (Brix, 1971):

1. Day-night temperature differential requirement.
2. No temperature differential requirement (but growth may respond to day or night temperatures).
3. Response to heat sum.

Different temperature optima and growth response between species suggests that each species is (genetically) adapted to its natural habitat. Within species with a wide natural distribution encompassing differing temperature conditions, selection processes may give rise to distinct genetic variation between populations. Thus these populations, or provenances, may also show differing responses in growth to varying temperature conditions.

While a large range of coniferous species have been investigated, there does not appear to have been any studies of *C. lanceolata* to date. This experiment therefore is an initial

look at the growth response of *C. lanceolata* seedlings from several provenances to different temperature treatments and will examine the differences in growth between temperature treatments and between provenances.

2. MATERIALS AND METHODS

Seed from the twelve provenances were soaked overnight and sown in trays with sieved (<4.75 mm) commercial potting mix and sand, and germinated at 24 °C. Germination was apparent from eight days after sowing, seedlings were then transplanted from 14 days after sowing into 200 ml plastic pots containing commercial potting mix with a three month supply of "Osmocote" fertiliser.

2.1 Provenance Material

Uneven germination in some provenances resulted in few seedlings for these provenances which consequently could not be analysed in this experiment. As a result seven provenances were represented in two temperature treatments, and three of these were also represented in a third treatment.

The seven provenances analysed in the experiment were: PV's 1 - 5, 9, and 10. Full details are given in appendix A. Several provenances could not be represented, however the provenances above give a reasonably good geographical and altitudinal range, as well as representation of a number of "growth zones" (China, Cooperation Group of Chinese fir, 1981b).

2.2 Treatment Conditions

Four weeks after sowing seedlings were placed in two controlled environment chambers (growth cabinets), at the Forestry Research Centre, Ilam. Conditions were as follows:

Treatment (TR):	1.	2.
16 hours light @:	28 °C	18 °C
8 hours dark @:	21 °C	11 °C
Relative humidity @:	68 %	42 %

In both cabinets lighting consisted of one hour of incandescent light followed by 14 hours of full light (220 μmol m^{-2} s^{-1} for TR1, 215 μmol m^{-2} s^{-1} for TR2), followed by another hour of incandescent light. Relative humidity was set to maintain a vapour pressure deficit of 12 millibars in each cabinet.

A third treatment (TR3) was carried out under glasshouse conditions which were under much less control. These were as follows:

Temperature:	Mean	20 °C (day), 18 °C (night), 19 °C (overall)
	Minimum	16 °C (mean), 10 °C (absolute)
	Maximum	24 °C (mean), 29 °C (absolute)
Light:	16 hours @	8 hours natural, 8 hours artificial
	Mean	150 μmol m^{-2} s^{-1}
	Minimum	2 μmol m^{-2} s^{-1} (absolute)
	Maximum	425 μmol m^{-2} s^{-1} (absolute)
Relative Humidity:	Mean	64 %
	Minimum	18 %
	Maximum	91 %

Seedlings were grown for 55 days in the above conditions. Provenances were represented in the treatments thus:

Treatments	PV
1. (28 °C/21 °C)	1, 2, 3, 4, 5, 9, 10
2. (18 °C/11 °C)	1, 2, 3, 4, 5, 9, 10
3. (Glasshouse)	1, 9, 10

Individual seedlings from PV's 7, 11 and 12 were also placed in the growth cabinets. Seedlings were randomly arranged within each treatment, watering was gravimetrically determined (sample pots were weighed and 20 ml of water was added to all pots when the sample pots had lost 20 g or more weight).

2.3 Measurements

Immediately prior to the start of the experiment between four to nine seedlings from each of the seven provenances were bulk harvested and oven dried for 48 hours at 70 °C; leaf (L), stem/root (R), and total (T) dry weights were recorded. Throughout the experiment individual seedlings from each provenance were harvested from each treatment at regular intervals (every 10 days for PV's 1, 9, 10 and every 11 days for PV's 2, 3, 4, 5) and measured for total height (H_t), number of leaves (N_l), length of longest leaf (L_l), and oven dry weights. The remaining seedlings were re-randomised after each 11-day harvest.

Two days before the end of the experiment three seedlings from each provenance were selected from each treatment and measured for photosynthesis (PS) using the LI-6200 portable photosynthesis system (LI-COR, Lincoln, Nebraska, USA). These seedlings were then measured for leaf area (A_l) with a Delta-T area meter, harvested and measured for H_t, N_l, L_l, shoot extension (H_S, distance from the cotyledons to the growing tip), and

oven dry weights S (shoot weight), C (cotyledon weight), L, R, T. The remaining seedlings were then bulked for each provenance in each treatment, and harvested.

2.4 Analysis

Analysis of variance (ANOVA) of seedlings in the final harvest was carried out for all the measured variables (H_t, H_S, N_l, L_l, L, S, R, C, T), and net photosynthesis (PS). Derived values leaf:total weight ratio (L:T), leaf area:total weight ratio (A_l:T), and leaf area:leaf weight ratio (A_l:L) were also analysed. The ANOVA format for a two factorial completely randomised design was as follows:

Source	Degrees of Freedom	
Temperature (TR)	1	2
Provenance (PV)	6	2
TR x PV	6	4
Error	28	18
TOTAL	41 [i]	26 [ii]

For the seven provenances in the two growth cabinets (i), and the three provenances present in all three treatments (ii). The third temperature treatment (glasshouse), statistically, cannot be analysed with the other treatments; however it is included for general comparison.

In addition relative growth rates for each provenance were calculated in each treatment. This was calculated using total dry weights with the equation:

$$\mathbf{RGR = (LogeT_2 - LogeT_1)/(t_2 - t_1)}$$

Where RGR = mean relative growth rate
T_2 = total dry weight at harvest 2
T_1 = total dry weight at harvest 1
t_2 = time of harvest 2
t_1 = time of harvest 1

(From Hunt, 1978)

However differences between the individual observations (harvests) for each provenance occasionally gave negative growth rates. Time series regression equations using all observations for each provenance in each treatment were therefore fitted in the form:

$$\mathbf{LogeT_t = \beta_0 + \beta_1(t)}$$

Where T_t = total dry weight at time t

β_0 = Log_e of initial total dry weight
β_1 = slope (or growth rate)
t = days

Mean relative growth rate for the experiment was taken as the slope of the equation, given on a g g^{-1} day^{-1} basis. The slopes were then compared using the separate slopes model in SAS.

3. RESULTS

Results demonstrated large differences in seedling growth (and development) between high (TR1) and low (TR2 and TR3) temperatures (see Plates 6.1 and 6.2); the regression equations for relative growth also clearly showed these differences. Provenance differences within treatments were not as apparent but were significant for some of the variables measured.

3.1 Analysis of Variance

Temperature: All variables showed *highly* significant differences between TR1 and TR2 ($p = 0.0001$), with most showing increases at the higher temperatures; negative correlations were seen in C and PS.

In general this trend was also demonstrated between TR1 and TR3 except in A_1:T and A_1:L where values were significantly higher in 3 then in 1. There were no significant differences between TR2 and TR3 except in C (lower in 3), A_1, A_1:T, A_1:L and L:T (all greater in TR3). This indicates that at higher temperatures proportionately more growth takes place in the leaf tissue compared to the stem and root.

Table 6.1 gives the mean values for each variable in each treatment.

It would appear that C is inversely related to growth, perhaps reflecting different stages of plant development. In TR1 the plants are at a "later" stage of development than in TR2; leaf expansion is larger and numbers of leaves are greater. At this later stage of development it would be expected that the plant would rely proportionately more on the primary leaves for photosynthesis, resulting in translocation away from the cotyledons and eventual senescence of the cotyledons.

While most variables were not statistically different overall from TR2, TR3 appears to give a response intermediate between TR1 and TR2. This is most clearly seen in C, A_1, A_1:L and L:T which are significantly different.

Provenance: Differences between provenances were not as striking as between temperature treatments. Nevertheless significant differences ($p = 0.01$ level) were present

between PV's 4 and 2 for three variables, R, T and A_l (all greater in PV4). Provenance means are given in Table 6.2.

Other variables while not significantly differing between provenances also indicate the faster growth trend of PV4 over PV2 in greater H_t, N_l, L, and S. However this was reversed for all ratio measures and PS, with PV2 having larger values than PV4. A similar PS response was observed between the two temperature treatments, suggesting that growth is negatively correlated with PS; however there was no negative correlation for any of the ratios in the treatments.

Temperature x Provenance Interaction: Interaction was significant for leaf number ($p = 0.05$), root/stem weight, shoot weight, total weight, leaf area ($p = 0.01$). One way analysis of variance showed significant differences in TR1 for R, T, A_l and in TR2 for N_l (Table 6.3). The trend of difference between PV's 4 and 2 is seen in TR1 although at TR2 this is not evident.

3.2 Relative Growth Rates

As noted above a time series regression model was used to give mean relative growth rates (RGR). Although this does not strictly give an RGR measure as per the equation given by Hunt, in all cases the model fitted the points very closely for all temperature x provenance combinations (all r^2 values > 0.9) and all regressions were highly significant ($p = 0.0001$). The close fit justifies using the slope of each equation to give a measure of RGR over the whole experiment, equation parameters and r^2 values are given in Table 6.5.

Figure 6.1 shows RGR's for each treatment, it can be seen that in the higher temperature PV4 has a noticeably higher RGR than PV2 (as indicated in the analysis of variance), Figure 6.2 shows this difference. In fact PV2 had significantly less RGR (as approximated by $ß_1$ in Table 6.5) than all other provenances. There were also significant differences in TR2; in this case PV3 has the highest RGR (Figure 6.3) while again PV2 had the lowest RGR. Differences between TR1 and TR2 are readily apparent (Figure 6.4).

4. DISCUSSION

4.1 Growth Response to Temperature

Optimum temperature: Results demonstrated the increase of growth from 18/11 °C to 28/21 °C for all provenances. This is not unexpected given the temperature conditions in *C. lanceolata*'s natural range which reaches mean temperatures of 28 - 30 °C in July and August (Hsieh, 1973; China Cooperation Group of Chinese fir,1981b). It would

appear that *C. lanceolata* is well adapted to high temperatures. Rapid growth of *C. lanceolata* occurs between June and September (Cai *et al.*, 1984) when mean monthly temperatures range from about 22 to 30 °C generally, and 25 - 30 °C in high yield areas (Wu, 1984).

However it is not apparent as to how close the level and conditions used in this experiment (28/21 °C) is to *C. lanceolata*'s optimum. While there is a good response to this level, which approximates those of the two warmest months, this may just reflect evolutionary adaptation to its environment: Hellmers and Rook (1973) state that the native habitat of a species should not be assumed to define optimum conditions for growth. Provenance testing of other species has also shown that native trees have not grown as well as those from 50 to 500 miles away (Wright,1976). Furthermore phenological aspects may be important. In many species cessation of growth is closely associated with the warmest part of the growing season either by formation of over-wintering buds and/or inducing the accumulation of growth inhibitors (Hellmers, 1962, Kramer 1957b).

A number of studies of growth of tree seedlings, mainly temperate species, show varying, but generally lower optimum temperatures than the level tested in this experiment. *Pinus taeda* appears to be an exception with optimum growth occurring at high day and low night temperatures; 30/17 °C and 23/11 °C treatments gave the best growth (Kramer, 1957a).

Pseudotsuga menziesii conversely appears not to require such day-night differentials and has a broad optimum temperature range of 18 - 24 °C. This may in part be related to its wide distribution which covers a range of temperature regimes (Brix,1971). Similar temperature requirements are seen in *Tsuga heterophylla*, although the temperature optimum is not as broad, occurring around 18 °C (Brix,1971).

Sequoia sempervirens, a species that comes from the same family as *C. lanceolata* also does not seem to require a large day-night differential with best growth at a 19 °C day temperature (Hellmers 1966). Conversely, growth in *Pinus radiata* is significantly related to cold night temperatures (5 °C) with best growth occurring with day temperatures of 17 and 23 °C. This closely matches temperature levels in its native habitat (Hellmers and Rook, 1971). *Picea engelmannii* seedlings also appear to respond best to a night temperature of 23 °C. Day temperature was not as important, but best growth occurred when this was at 19 or 23 °C (Hellmers et al., 1970), similar to *Sequoia sempervirens*, in terms of temperature levels.

SEE ERRATA

Pinus resinosa produced greatest growth for primary needles at 20 °C (Kozlowski and Borger, 1971), this being similar to northern provenances of *Pinus sylvestris* which had optimum temperatures for formation of stem unit primordia and shoot elongation of 18 to

21 °C (Juntilla, 1986). *P. brutia* a more sub-tropical species appears to respond more to heat-sums rather than particular temperatures (Hellmers, 1962), as do *P. attenuata* and *P. sabiniana* (Lanner, 1964).

As can be seen from the above examples, temperature optima for temperate conifers mostly fall between 17 - 24 °C. Higher temperatures result in lowered growth, perhaps due to thermal denaturation of enzymes controlling the growth processes (Fitter and Hay, 1981) although this seems unlikely at the level of temperatures considered. Growth is more likely to be limited by competition between processes in the conversion of food into new tissue and use of food in respiration (Kramer 1957b). Translocation of sugars and transport of water to and from root to shoot zones are other possible factors (Chalupa and Fraser, 1968; Hellmers, 1963; Kramer,1957a; Went, 1955); increasing temperature has been observed to cause decreased translocation (Went, 1955) and associated decreased growth (Chalupa and Fraser, 1968).

In this experiment it would appear that *C. lanceolata* responds better to higher temperatures in terms of growth as would be expected from a sub-tropical species. However the exact requirements (optimum temperature, differential requirements, heat-sums) are unknown.

Photosynthesis: Net photosynthetic rate (the balance of CO_2 uptake between gross photosynthesis and respiration) represents a measure of growth (net carbon assimilation) and as such this follows the bell shaped response to temperature.

Photosynthetic response was negatively correlated with growth (*i.e.* there was less CO_2 assimilation per unit of leaf area over time at the higher temperature than at the lower temperature treatment - Figure 6.5). It would be expected that optimum temperatures for photosynthesis are similar to day-time temperatures at which the species normally grows (Salisbury and Ross, 1978); for C3 plants this is reflected in a generally flat, broad temperature response curve between 15 and 30 °C. While this is usually the case (*e.g.* Tranquillini et al., 1986; Hawkins, 1989; Kramer, 1957a), the relationship between optimum temperatures for photosynthesis and growth *per se* is not as straight forward.

Negative correlation between photosynthesis and growth rate has been observed in *Pinus taeda* and *P. sylvestris* (Kramer and Kozlowski, 1979), similarly optimum temperatures for photosynthesis has been reported at levels much lower then that for growth in *Pseudotsuga menziesii* (Doehlert and Walker, 1981) and for European tree species (Kramer,1957b). It is possible that for *C. lanceolata* the optimum for photosynthesis occurs at a lower temperature than for actual growth.

Kramer and Kozlowski (1979) suggest that mutual shading of needles or anatomical differences in needles are possible causes of this negative relationship. This is borne out

by the leaf area/leaf weight ratios (Table 6.1). At higher temperatures with faster leaf growth, the higher ratio indicates that for a given leaf area, there is less leaf material. This implies thinner leaves and subsequently less photosynthetic tissue (such as chloroplasts) per unit area of leaf. This would seem to account for the lower photosynthetic *rate* and chlorophyll content has been closely correlated with CO_2 uptake under controlled conditions (Kramer and Kozlowski, 1979). Thus while photosynthetic rate was reduced, perhaps due to a lower concentration of photosyntheticaly active areas, absolute photosynthesis (PS^*A_l) is greater at the higher temperature treatment due to the greater amount of leaf area present (Table 6.4). Growth of the species as a whole is affected by starting weight, and RGR; RGR in turn is derived from leaf area ratio and net photosynthetic rate. Thus at the higher temperature, increased growth is due to a proportionately greater increase in leaf production over a decrease in photosynthetic rate. Very large increases in L and A_l in Table 6.1 appear to be in agreement with this.

There are, however, other factors which may account for this result of increased photosynthesis at the lower temperature. Measurement was carried out during a phase of rapid leaf expansion; in general photosynthesis is assumed to increase and reach a maximum when leaves are fully expanded (Schaedle, 1975). However during the initial phase of rapid seedling growth conditions fluctuate and are variable compared to when growth flattens out. Measurement before this later phase may be confounded by these fluctuating conditions (I M^{c}Cracken, pers. comm.).

Another possible cause may be the CO_2 concentration in the growth cabinets; in the lower temperature treatment CO_2 concentration was on average 440 parts per million (ppm) compared to 400 ppm in the higher temperature treatment. This would have been reflected in greater intercellular CO_2 concentrations in the lower temperature, which generally results in enhanced photosynthesis (Raschke, 1975). Whether the difference in levels significantly affected the photosynthetic rate or not cannot be determined from this experiment.

4.2 Growth Differences Between Provenances

As shown in the results, growth differences between provenances were not significant except for N_l, R, T, and A_l. Of these R, T and A_l were only significant in TR1 while N_l was significant only in TR2. Overall provenance differences were seen in the same variables as for the provenance x temperature interaction in TR1, suggesting that this temperature treatment had the dominant effect in the overall analysis.

TR1: In TR1 consistent differences were seen between PV's 4 and 2, with PV4 exhibiting greater growth in both ANOVA of the three variables, and RGR. In terms of RGR, PV2 was significantly less than all other provenances.

A similar trend (with that seen between temperature treatments) of decreased photosynthetic rate with increased growth is evident. From Tables 6.3 and 6.5, PV4 has greater RGR, leaf area, total dry weight and leaf production than PV2: Conversely PV2 exhibits a higher photosynthetic rate than PV4 (Figure 6.5). It is therefore reasonable to assume that growth differences between provenances arose out of rates of leaf production rather than rates of photosynthesis.

There is no apparent trend in geographical factors that account for the increased growth of PV4 over PV2. More surprisingly, both provenances occur in the central zone of *C. lanceolata*, which is reported to be the best zone for growth and PV2 occurs in the mountain sub-region of this zone which is considered to be one of the best sub-regions for growth (China, Cooperation Group of Chinese fir, 1981b). On a purely geographical basis it would seem more likely that differences would be seen between the provenances from the northern zone (PV's 9 and 10), and the central provenances (PV's 1-5). This is certainly the case in longer term provenances tests (Chen *et al.*, 1980).

It is possible that the difference may be an artefact of the experiment due to the short growing period (55 days) and the small number of observations for each provenance. Since summer temperatures in June and July are relatively uniform throughout the whole of sub-tropical China it is surprising that growth differences would be significant at this temperature. Growth differences are due to both growth rate and length of growing season. This perhaps explains why there appears to be no definite north-south trend which is often the case in northern temperate species (Wright, 1976). Certainly a longer growing period and/or more observations per provenance would give a clearer trend.

TR2: Leaf number, N_l was the only variable which showed significant differences with PV10 having more leaves compared to PV's 2, 5 and 9. Again it is not readily apparent as to why only one growth measure should be significant. It is inviting to speculate that the northern provenances would be better adapted to the lower temperature and as such exhibit better growth; although adaptation to low temperatures does not necessarily entail faster growth. Even if this is the case it does not explain why PV9 was amongst the least productive - even in the non-significant variables (Table 6.3). In terms of RGR, PV's 3, 10 and 1 are also greater than PV2 (Table 6.5). That PV2 was the worst performing provenance at both temperatures suggests that this provenance is overall the slowest growing provenance in this study. However there is no clear reason why this should be the case (see above discussion).

Unfortunately a detailed discussion on the provenance differences in growth is restricted by the lack of knowledge of the provenances; while geographically the separation of PV's 2, 4 and 10 is quite large there may be relatively small differences in genetics as shown in chapter V. However provenance tests in China indicate high variability between populations with adaptation to site and climate (Pan *et al.*, 1983). Furthermore it seems

that the best provenances originate from the central zone and more specifically to the Nanling mountain range (Guangdong Provenance Trial Cooperation Group of Chinese fir, 1986; National Collaborative Research Group on Provenances Trial of Chinese fir, 1988): PV's 1, 2, 3 and 5 originate from this region; thus it is surprising that PV2 should exhibit the poorest growth.

5. SUMMARY

This experiment clearly showed that growth of *Cunninghamia lanceolata* seedlings dramatically increased when temperature was increased from an 18/11 ^{o}C regime (TR2) to 28/21 ^{o}C (TR1). Growth increased by almost 260 per cent in total dry weight; similar increases were observed in most other growth measures except for cotyledon dry weight and photosynthesis which were negatively correlated with increased growth.

A third, less controlled, treatment, averaging 20/18 ^{o}C (TR3), was similar in response to TR2; however variables were consistently intermediate between the other two treatments. A true comparison could not be made with this treatment as light, relative humidity and temperature were not under the same degree of control.

These results suggest that the optimum temperature for seedling growth lies somewhere above 20 ^{o}C and possibly near 28 ^{o}C, particularly as this is similar to mean summer temperatures in its native range and especially so over the period of rapid growth. Given that most temperate conifers have a temperature optimum between 17 and 24 ^{o}C, it is likely that *Cunninghamia* being sub-tropical would have a slightly higher optimum.

The photosynthetic optimum appears to be lower than that for overall growth and while this is not usually the case, lower temperature optima for photosynthesis have been reported in some species. Although actual growth response to high temperatures is evident in this experiment the photosynthesis measurements may have been more meaningful if the experiment had been extended until leaf expansion had ceased and internal leaf conditions had stabilised.

Provenance differences were less significant than temperature; most apparent difference was observed between PV4 and 2 in TR1, with PV4 exhibiting faster growth. There is no readily apparent reason as to why PV4 should be faster growing and again this difference may be not be significant after the early seedling growth stage; longer duration of the experiment may have given a clearer indication.

Table 6.1: Mean Values for Growth Measures at Different Temperatures

Growth Measure	Temperature Treatment[1]						
	1.[28/21 °C]		%incr.[2]	2.[18/11 °C]		3.[20/18 °C]	Rank
Ht (mm)	136.0[a]	(136.9[a])	28	106.5[b]	(103.1[b])	(112.4[b])	1 > 3, 2
H_S (mm)	30.2[a]	(30.8[a])	175	11.0[b]	(10.8[b])	(11.9[b])	1 > 3, 2
L_l (mm)	74.7[a]	(78.0[a])	114	34.9[b]	(33.2[b])	(39.8[b])	1 > 3, 2
N_l	75[a]	(73[a])	97	38[b]	(41[b])	(43[b])	1 > 3, 2
L (g)	0.1594[a]	(0.1581[a])	358	0.0348[b]	(0.0355[b])	(0.0405[b])	1 > 3, 2
R (g)	0.0552[a]	(0.0486[a])	172	0.0203[b]	(0.0205[b])	(0.0196[b])	1 > 2, 3
S (g)	0.0171[a]	(0.0163[a])	317	0.0041[b]	(0.0043[b])	(0.0032[b])	1 > 2, 3
C (g)	0.0034[a]	(0.0031[a])	-45	0.0062[b]	(0.0058[b])	(0.0042[c])	2 > 3 > 1
T (g)	0.2350[a]	(0.2261[a])	259	0.0654[b]	(0.0661[b])	(0.0675[b])	1 > 3, 2
A_l (mm^2)	3289[a]	(3203[a])	481	566[b]	(592[b])	(987[c])	1 > 3 > 2
$R_{A:L}$ ($mm^2\ g^{-1}$)	20936[a]	(20422[a])	29	16234[b]	(16722[a])	(25257c)	3 > 1 > 2
$R_{A:T}$ ($mm^2\ g^{-1}$)	14159[a]	(14270[a])	65	8584[b]	(8884[b])	(14921[a])	3, 1 > 2
$R_{l:T}$ ($g\ g^{-1}$)	0.6783[a]	(0.6997[a])	28	0.5288[b]	(0.5325[b])	(0.5938[c])	1 > 3 > 2
PS ($\mu mol\ m^{-2}\ s^{-1}$)	2.165[a]	(2.395[a])	-45	3.952[b]	(3.771[b])	(3.202[b])	2 > 3, 1

Notes: [1]values with the same letter are not significantly different at the 95% level. [2]% increase from treatment 2 to treatment 1.

n.b. values in parentheses are from the analysis of the three temperature treatments. See section 2.3 for definitions of variables.

Table 6.2: Mean Values for Growth Measures in Different Provenances

Growth Measure	Provenance						
	PV1	PV2	PV3	PV4	PV5	PV9	PV10
Ht (mm)	125	117	119	124	129	118	117
H_S (mm)	20	20	22	17	22	20	23
L_l (mm)	57	55	56	55	52	56	54
N_l	57	49	57	64	54	53	61
L (g)	0.1010	0.0846	0.0862	0.1190	0.0994	0.0959	0.0935
R (g)	0.0408^{ab}	0.0332^{b}	0.0322^{b}	0.0546^{a}	0.0405^{ab}	0.0293^{b}	0.0335^{ab}
S (g)	0.0113	0.0081	0.0108	0.0126	0.0117	0.0094	0.0101
C (g)	0.0046	0.0055	0.0042	0.0052	0.0052^{a}	0.0040^{a}	0.0048^{a}
T (g)	0.1577^{ab}	0.1314^{b}	0.1334^{ab}	0.1914^{a}	0.1567^{ab}	0.1387^{ab}	0.1419^{ab}
A_l (mm^2)	2048^{ab}	1616^{b}	1851^{ab}	2309^{a}	2024^{ab}	1973^{ab}	1672^{ab}
$R_{A:L}$ ($mm^2\ g^{-1}$)	18574	18391	19943	17618	18426	19341	17802
$R_{A:T}$ ($mm^2\ g^{-1}$)	11357	11070	12465	10251	11084	12329	11044
$R_{l:T}$ ($g\ g^{-1}$)	0.6026	0.5995	0.6181	0.5678	0.5914	0.6289	0.6167
PS ($\mu mol\ m^{-2}\ s^{-1}$)	2.932	3.347	3.122	2.717	2.976	3.147	3.170

values with the same letter (or no letter) are not significantly different at the 95% level.

See section 2.3 for definitions of variables.

Table 6.3: Mean Values for Growth Measures of Provenances at Different Temperatures

Measure	Temp.	PV1	PV2	PV3	PV4	PV5	PV9	PV10
N_l	1	73	63	71	94	75	71	75
	2	40^{ab}	34^{b}	43^{ab}	34^{b}	33^{b}	35^{b}	46^{a}
R (g)	1	0.0620^{ab}	0.0475^{ab}	0.0447^{ab}	0.0869^{a}	0.0612^{ab}	0.0400^{b}	0.0438^{ab}
	2	0.0197	0.0189	0.0198	0.0223	0.0198	0.0185	0.0233
T (g)	1	0.2522^{ab}	0.1964^{b}	0.1984^{b}	0.3176^{a}	0.2540^{ab}	0.2195^{ab}	0.2067^{ab}
	2	0.0632	0.0665	0.0685	0.0652	0.0593	0.0578	0.0772
A_l (mm^2)	1	3551^{ab}	2650^{b}	3065^{ab}	4129^{a}	3572^{ab}	3423^{ab}	2634^{b}
	2	544	582	637	489	476	523	710

values with the same letter (or no letter) are not significantly different at the 95% level. See section 2.3 for definitions of variables.

Table 6.4: Absolute Photosynthetic Rates at Different Temperatures

Temperature	PS (µmol m-2 s-1)	A_l (mm2)	PS_{abs} (µmol s-1)
28/21 °C	2.165	3289	0.0071
18/11 °C	3.952	566	0.0022
20/18 °C	3.202	987	0.0032

Table 6.5: Time Series Regression Equations for Each Provenance and Temperature

	Temperature Treatment								
	TR1			TR2			TR3		
PV	$ß_1$	$ß_0$	R^2	$ß_1$	$ß_0$	R^2	$ß_1$	$ß_0$	R^2
1	0.0751 [a]	1.3220	0.9955	0.0496 [a]	1.3024	0.9876	0.0464 [a]	1.303	0.9241
2	0.0638 [b]	1.7302	0.9805	0.0420 [b]	1.6850	0.9193			
3	0.0719 [a]	1.1773	0.9615	0.0506 [a]	1.2004	0.9545			
4	0.0782 [a]	1.3990	0.9836	0.0456 [ab]	1.4757	0.9600			
5	0.0733 [a]	1.3314	0.9815	0.0482 [ab]	1.3650	0.9600			
9	0.0726 [a]	1.4075	0.9882	0.0471 [ab]	1.3673	0.9823	0.0452 [a]	1.3131	0.9200
10	0.0721 [a]	1.4415	0.9897	0.0500 [a]	1.4333	0.9717	0.0458 [a]	1.4421	0.9624
All	0.0725	1.4067	0.9795	0.0477	1.4054	0.9717	0.0459	1.3524	0.9373

Parameters and R^2 values for regression equation $\mathbf{Log_e(T_t) = ß_0 + ß_1(t)}$.

n.b. $ß_1$ = Relative Growth Rate in g g^{-1} day^{-1} (slope of equation).

values with the same letter (or no letter) are not significantly different at the 95% level.

Figure 6.1a: Mean Relative Growth Rates

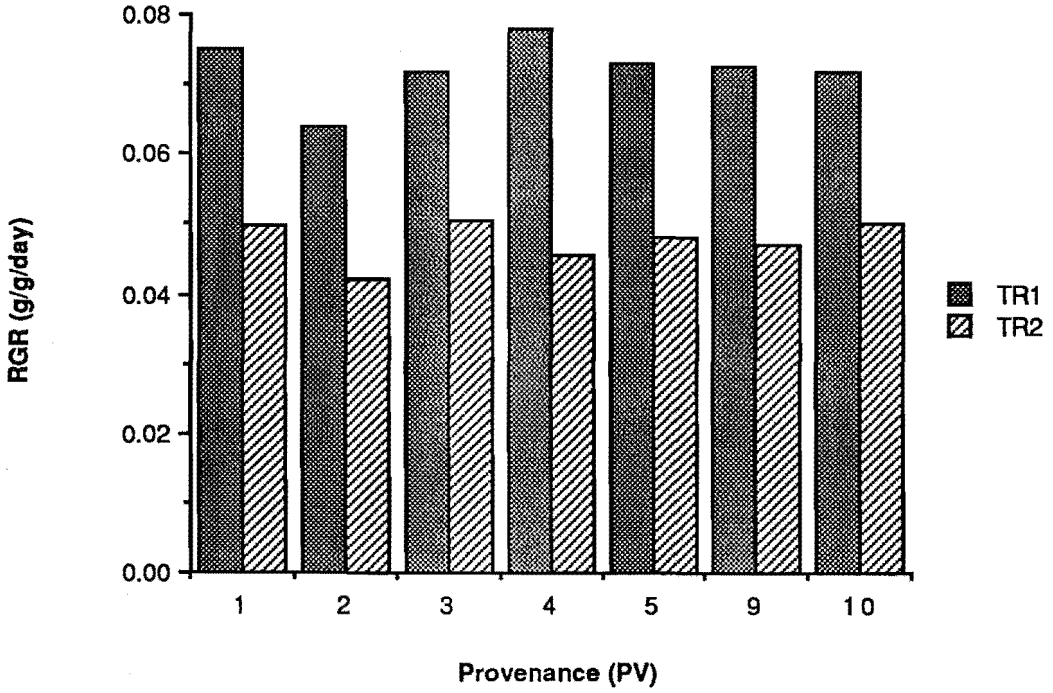


Figure 6.1b: Mean Relative Growth Rate (3 Temperature Treatments)

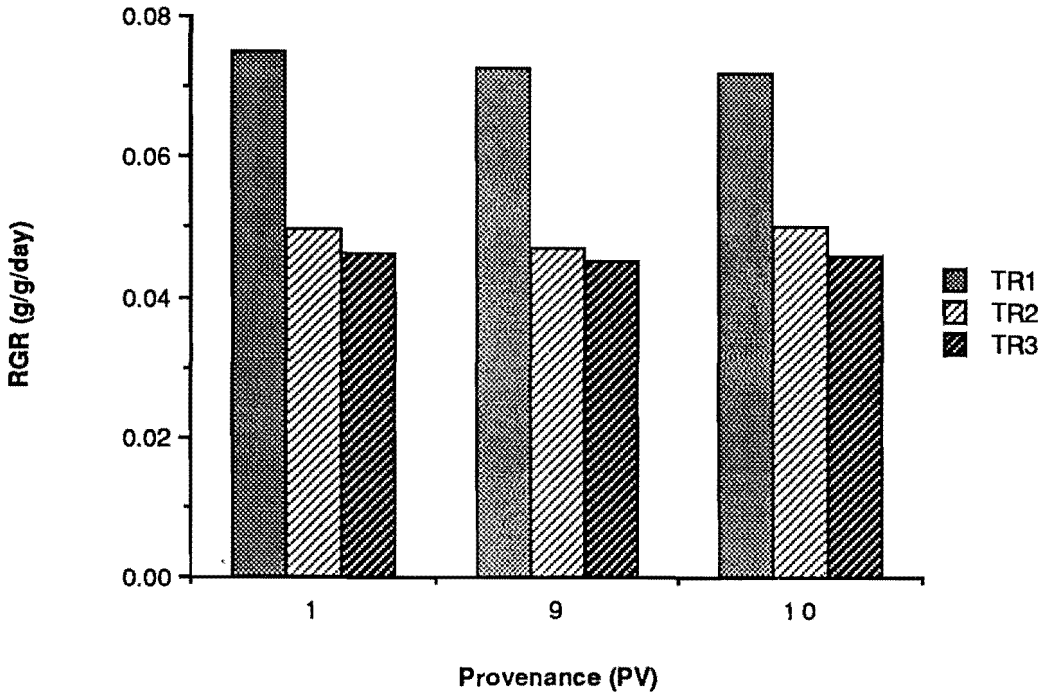


Figure 6.2: Regressions (Best and Worst RGR) for Treatment 1

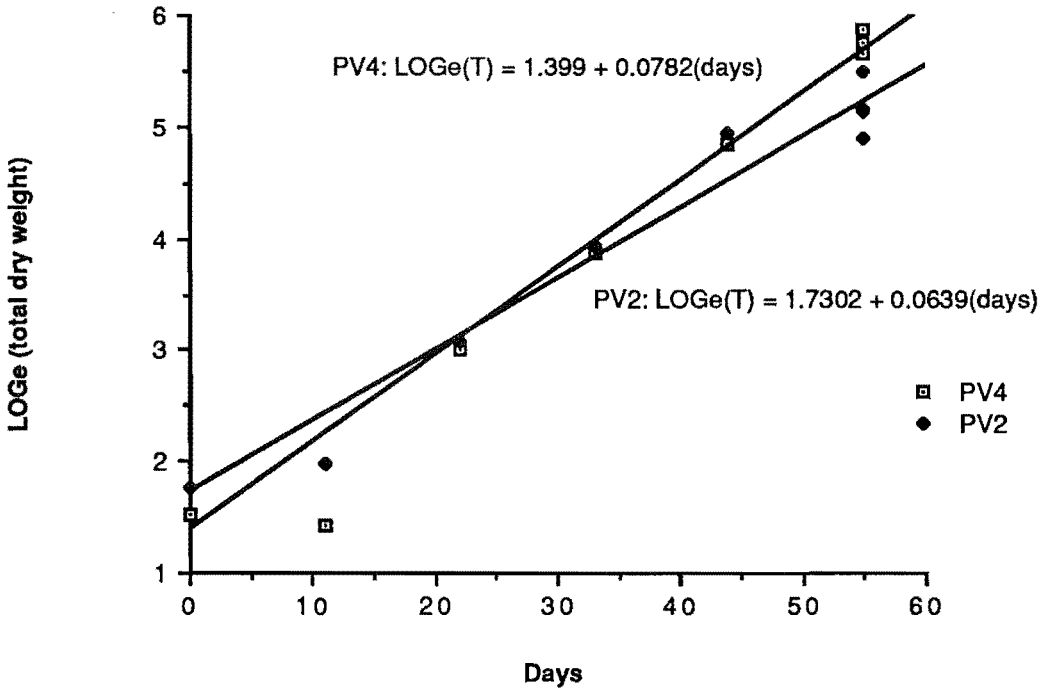


Figure 6.3 Regressions (Best and Worst RGR) for Treatment 2

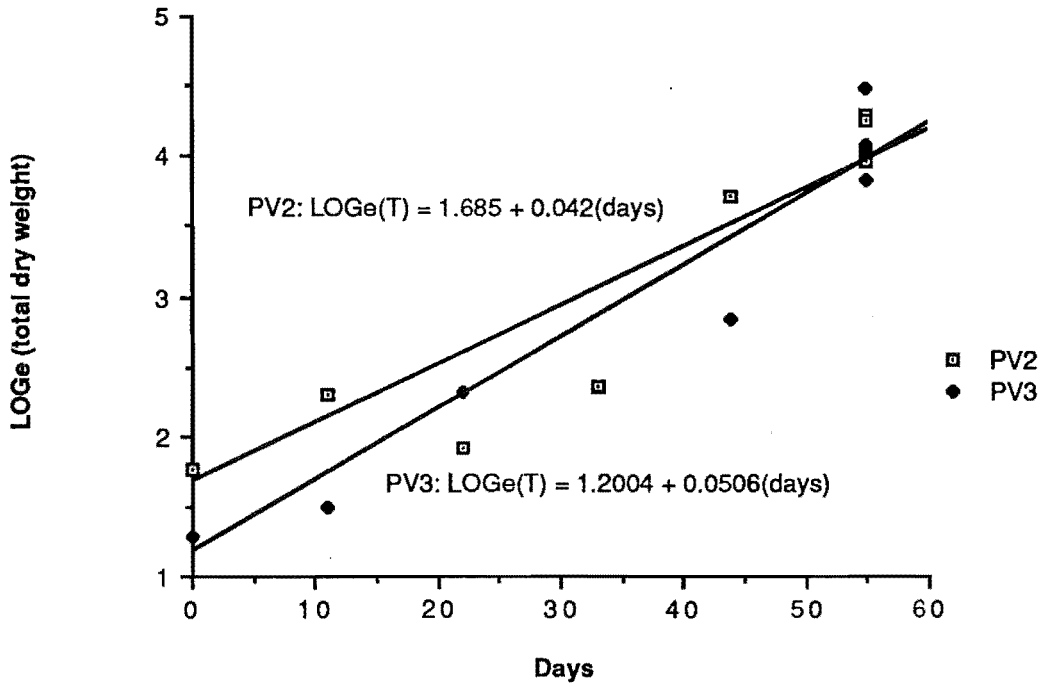


Figure 6.4: Regressions for PV1

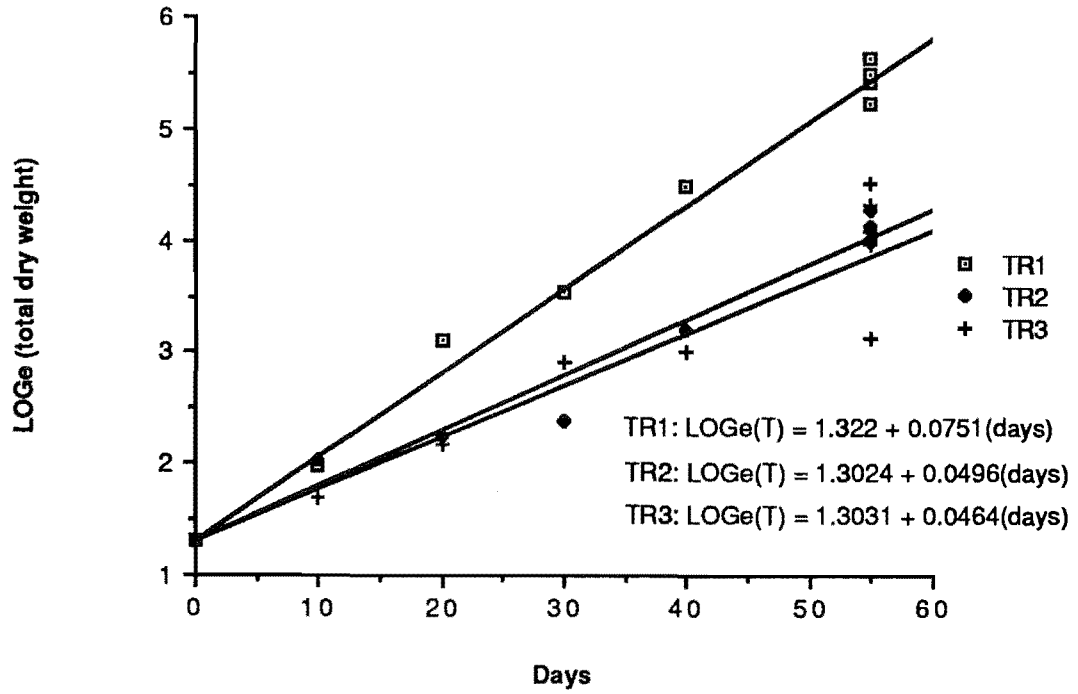


Figure 6.5 Net Photosynthesis

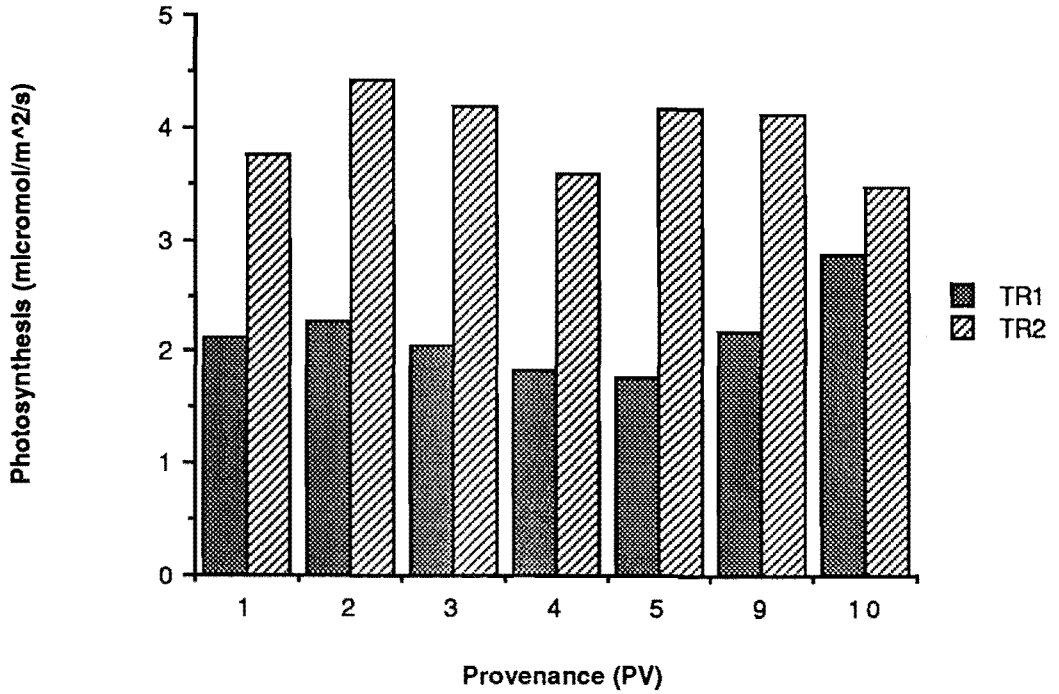


Plate 6.1: Seedling Growth Response to Several Temperature Treatments, PV1

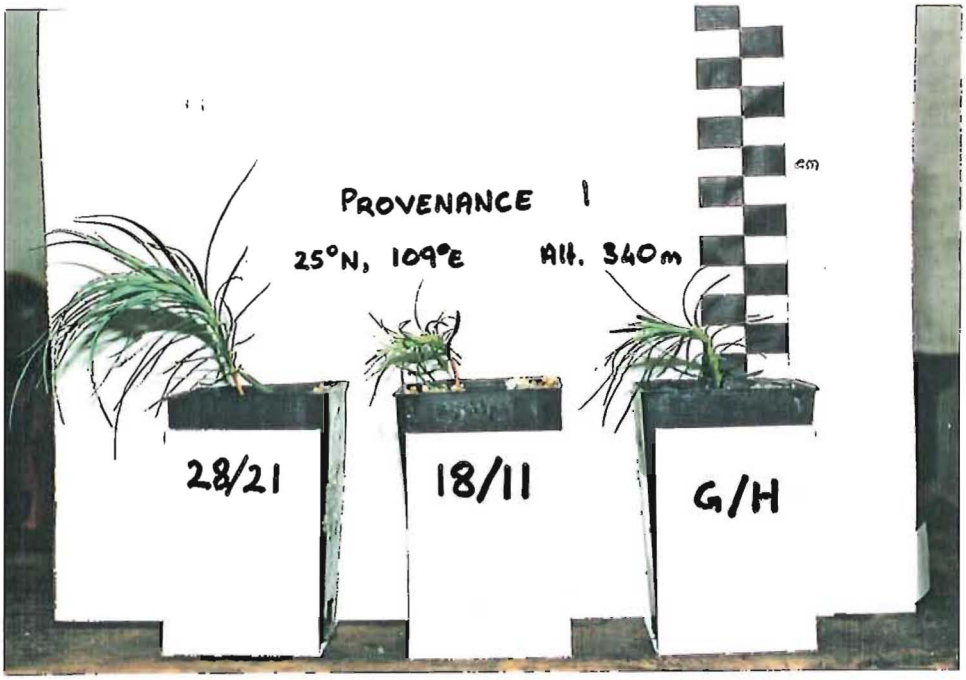
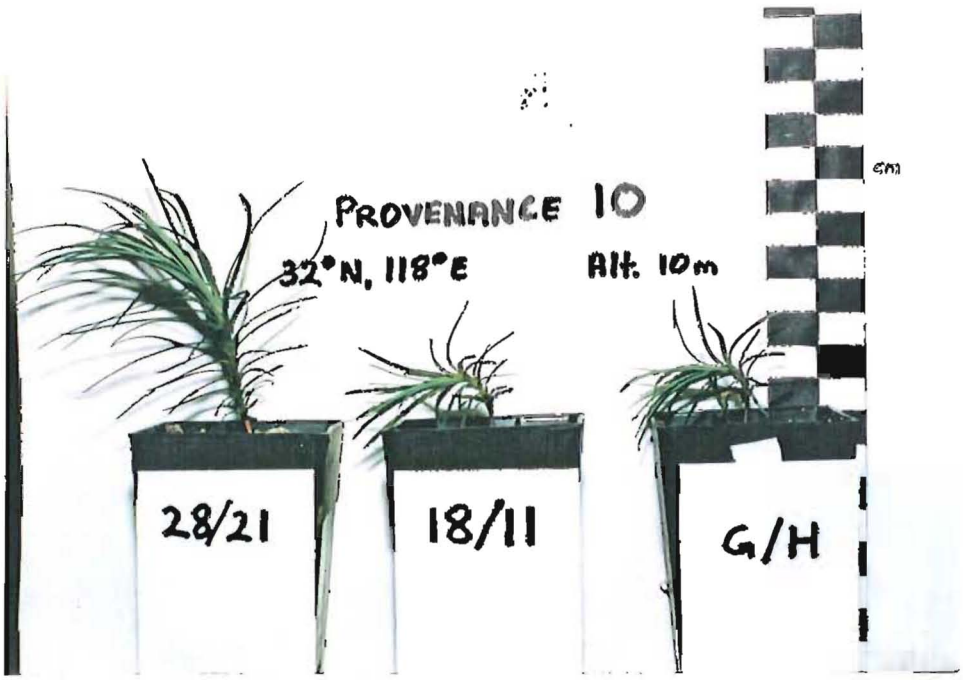


Plate 6.2: Seedling Growth Response to Several Temperature Treatments, PV10



CHAPTER VII

PHOTOSYNTHESIS AND GROWTH RESPONSE OF *Cunninghamia lanceolata* AND *Pinus radiata* SEEDLINGS UNDER DIFFERENT TEMPERATURE AND LIGHT TREATMENTS

1. INTRODUCTION

In considering a new species' potential for commercial use, a comparison with existing commercial species must be made. *Pinus radiata* is the main commercial tree species used in New Zealand and has been examined in depth. It is however considered unsuitable in China due to climatic limitations (high summer temperature and rainfall, and/or cold winters) typical of eastern continental land masses (NZFS, 1985). *C. lanceolata* on the other hand while obviously adapted to such continental climates has shown that it can be grown in other climate conditions. From other experiments carried out in this study it is apparent that out of season frosts, low water availability and temperature have a marked effect on growth and are likely to be important factors in New Zealand.

A direct comparison of growth rates of both species has not been made, either at the juvenile or mature stage. However height data from New Zealand grown stands of *C. lanceolata* is available and can be compared with those of *P. radiata* from similar areas. Volume growth is less reliable as this depends on height and basal area; basal area is strongly influenced by site, fertilising, stocking and thinning practices. Height is not affected by thinning or stocking (Goulding, 1986) and so is a better indication of comparative growth rates of the two species.

Mean heights of *C. lanceolata* at age 25 years grown in Rotorua are 12.2-14.3 m (see chapter XIII). *P. radiata* grown in Rotorua on relatively poor sites (site index of 24) has a mean top height of approximately 30 m at age 25 years and on better sites near Whakarewarewa (site indices of 28-35), has mean top heights of 33-40 m (Burkhart and Tennent, 1977); at this stage then *P. radiata* has grown over twice as fast as *C. lanceolata.* Although this is not a wholly valid comparison, and may not reflect seedling growth, the indication is that absolute growth of *P. radiata* is considerably greater than that of *C. lanceolata* under New Zealand environment conditions.

In the previous temperature experiment, *C. lanceolata* seedlings showed a significant increase in growth at 28/21 ^{o}C compared with 18/11 ^{o}C. While this demonstrated the species' preference for high temperatures, this may have been due to high day

temperature, high night temperature, or small day-night differential. In this experiment the performance of both *C. lanceolata* and *P. radiata* seedlings were compared at two temperature levels; one being favourable for *C. lanceolata*, the other favourable for *P. radiata*. The relative growth rates of each species within each temperature were compared, as well as photosynthesis under different light intensities at each temperature.

2. MATERIALS AND METHODS

2.1 Material

Six month old seedlings of both *Cunninghamia lanceolata* and *Pinus radiata* were used. *C. lanceolata* seedlings were from PV2 seedlot. Seeds were stratified and sown under glass. Seedlings were then transplanted into pots with commercial potting mix and slow release fertiliser. *P. radiata* seedlings were taken from an open grown nursery site at FRC, Rangiora two weeks prior to the experiment. Seedlings were similarly potted up with commercial potting mix and fertiliser.

Although seedling age was similar for both species, mean initial dry weight of *C. lanceolata* was 3.838 g compared to 1.560 g for *P. radiata*, almost 2.5 times greater. This was most likely due to growing conditions. *C. lanceolata* seedlings were grown in a heated glasshouse with adequate nutrients and water supply. The *P. radiata* were from open grown nursery beds and therefore subjected to more environmental variation.

2.2 Treatment Conditions

Seedlings were placed into two growth cabinets set at different temperatures (similar to Chinese or New Zealand summer temperatures) and grown for five weeks under the following treatments:

Cabinet 1 (Chinese): TR1

Day conditions	28 °C	70% RH	16 hours
Night conditions	13 °C	70% RH	8 hours

Cabinet 2 (New Zealand): TR2

Day conditions	20 °C	55% RH	16 hours
Night conditions	5 °C	55% RH	8 hours

Relative humidity (RH) was set to obtain a vapour pressure deficit of 12 mbars in each cabinet. Seedlings were watered daily as appropriate to ensure that water was not limiting for growth and/or photosynthesis.

After five weeks growth cabinets were set up to provide a range of light intensities by placing shade cloth between the seedlings and the lighting rig. Photosynthesis measurements were then taken. At the end of each day of measurement, sample seedlings were biomassed. Measured light levels ($\mu mol\ s^{-1}\ m^{-2}$ or μE) were as follows:

		Cabinet 1	Cabinet 2
Day 1:	Full light	580	640
	1 x 30% shade cloth	345	360
Day 2:	1 x 50% shade cloth	235	260
	1 x 75% shade cloth	160	160
Day 3:	2 x 75% shade cloth	50	55
	2 x 75%, 1 x 50%	30	30
	No light	0	0

2.3 Measurements

Six seedlings from each species were biomassed, for relative growth analysis, at the start of the experiment. Three more harvests, consisting of three seedlings of each species from each treatment, were carried out over the five weeks of the experiment.

After five weeks, four sample seedlings of each species from each treatment were measured for photosynthesis and biomassed at the end of each day. Leaf area calculations for photosynthesis were made with a Delta-T area meter. Two photosynthesis measurements per seedling were made on sample seedlings at each change in light after an initial settling period of $^1/_2$-1 hour. For *P. radiata* needles, a correction of π was applied to convert area of a single sided leaf to total surface area of pine needles (Grace, 1987). However due to high mortality of *P. radiata* in cabinet 1 only two sample seedlings were used each day.

For final growth analysis, dry weights (stem, S; leaf, L; root, R components and totals, T) and derived ratios (S:T, L:T, R:T, S:L, S:R, L:R) were taken for each seedling. Final growth analysis between temperatures was compared within each species. Relative growth analysis curves were compared between species and temperature. Photosynthesis responses were compared between light levels, and compensation points estimated for each species.

2.4 Analysis

Relative growth rate (RGR) was analysed by linear regression using $\log_e$ transformed biomass measurements of T (lnT), S (lnS), L (lnL), and R (lnR). The model was of the form:

$$\mathbf{Log_e(T_t) = ß_0 + ß_1(t)}$$

Where T_t = dry weight at time t
$ß_0$ = Log_e of initial dry weight
$ß_1$ = slope (or RGR)
t = days

For each species and temperature condition.

Mean relative growth rate for the experiment was taken as the slope of the equation, given on a g g^{-1} day^{-1} basis. Because there were fewer radiata seedlings harvested in the 28 ^oC treatment the group regression format was as follows:

Group	Total df	Residual df
Chinese fir, Cabinet 1 (C28)	26	25
Chinese fir, Cabinet 2 (C20)	26	25
Radiata, Cabinet 1 (P28)	21	20
Radiata, Cabinet 2 (P20)	26	25

The slopes were then compared using the test for common slopes; each group was compared with each other.

Because of inherent species differences in starting size and biomass distribution, overall growth in terms of biomass components was measured within each species separately. Derived ratios were compared between species and temperatures.

Final growth analysis was measured from the biomasses of the final harvest seedlings, pooled over the last three days. The ANOVA format was as follows:

Source	Degrees of Freedom		
Species (SP)	1		
Temperature (TR)	1	1	1
SP x TR	1	-	-
Error	39	22	18
TOTAL	42 [i]	23 [ii]	19 [iii]

[i] For biomass components
[ii] For derived ratios of *C. lanceolata*, and [iii] For derived ratios of *P. radiata*

Photosynthetic rates at different light levels were plotted for each species at each temperature. Light compensation point for each seedling was estimated by linear interpolation between the smallest positive and negative (nett) photosynthesis

measurements and compared by ANOVA. Photosynthesis was also compared by ANOVA at each light level.

For the purposes of analysis, light levels were grouped by shading regimes, even though levels *per se* differed between cabinets. Differences were slight or non-existent at lower light levels, while at higher levels photosynthesis exhibited a relatively broad and flattened response (see Figure 7.3). Thus comparison between cabinets (by shading regimes) was considered to be acceptable.

3. RESULTS

3.1 Relative Growth Rate

Mean RGR's and R^2 values are shown in Table 7.1. Regressions for each species, and for each SP x TR combination are shown in Figures 7.1 and 7.2. There were significant differences; RGR was greatest in C28, then C20, P28, and least in P20 for all four variables. A highly significant difference was also seen between C20 and P20 for lnL. Significant differences ($p = 0.05$) were seen between C28 and P28 for lnT, lnL and lnS; and also C20 and P20 for lnT.

A consistent species difference, with *C. lanceolata* having greater RGR than *P. radiata* regardless of temperature, was evident. Data were therefore pooled and regression lines by species were compared. Highly significant differences were seen in all four variables. R^2 values were high (0.739-0.867) indicating that the regressions were reasonable estimations of RGR.

3.2 Final Growth

Biomass components.

Mean values are given in Table 7.2, P values are given in Table 7.3. There were significant and highly significant differences between temperature for *C. lanceolata* in T, S, and R (but not in L). Differences were also significant between temperatures for *P. radiata* in T, R, and L but not in S.

In all cases biomass production was greater in the TR1 (cabinet 1).

Derived ratios.

Mean values are shown in Table 7.4. Highly significant ($p = 0.0001$) species differences were observed in all ratios except L:T, the species difference was significant ($p = 0.05$) for this ratio. *P. radiata* had a greater proportion of above ground biomass

allocation, and conversely, *C. lanceolata* had a greater proportion of below ground (roots) biomass allocation.

Temperature differences were significant for R:L, R:T, and L:T. TR1 showed higher values of R:L and R:T, this was opposite for L:T. There were significant SP x TR interactions for S:L and L:T.

3.3 Net Photosynthesis

Mean values at given light levels are shown in Table 7.5, P values in Table 7.6.

C. lanceolata had highly significantly greater photosynthesis rates than *P. radiata* at all light levels other than complete darkness (0 μE). Temperature had less effect on photosynthesis: The trend was for greater photosynthesis at TR1 except at complete darkness where respiration was greater at the higher temperature. Differences were significant at full light (580/640 μE) and 2 x 75% shade (50/55 μE), and highly significant at 30% shade (345/360 μE).

Species x temperature interaction was also highly significant from 30% shade down to 75% shade (345/360-160 μE), and significant at full light and 2 x 75% shade. Photosynthesis light curves for each SP x TR are shown in Figure 7.3.

Light compensation points were estimated from individual seedling measurements and so were able to be analysed in normal ANOVA form. Species differences were highly significant ($p = 0.0032$), with *C. lanceolata* having a lower light compensation point (20.2 μE) than *P. radiata* (49.6 μE). There was no significant difference between temperatures ($p = 0.4944$) or SP x TR ($p = 0.1065$). Light compensation points are given in Table 7.7.

4. DISCUSSION

4.1 Growth Responses

Species: While temperature showed significant differences the most striking difference was between species. Derived ratios were highly significant (or significant) but these are of little use in terms of growth, merely reflecting the difference in allocation of biomass between species. As initial starting size was different between species, RGR is used to account for this. Although starting sizes were different, seedling age was similar and hence the comparison is still valid in terms of growth phase within the species' life cycles.

By pooling temperatures within species a direct species comparison was obtained where for all mean RGR values *C. lanceolata* was highly significantly greater than *P. radiata.*

This is of interest as this implies that *C. lanceolata* is inherently a faster growing species, at least at seedling stage. How this relates to absolute growth rate at tree maturity is unclear as two factors are involved: 1) length of growing season, and 2) absolute growth rate during the season (Sweet and Wareing, 1968b). Similarly the components of RGR; net assimilation rate (NAR) and leaf weight ratio (LWR), cannot be estimated as leaf structures between the species differ markedly and hence leaf weight may not be valid for NAR (Sweet and Wareing, 1968a).

RGR's have been shown to differ between species (Pollard and Wareing, 1968; Sweet and Wareing, 1968a) but this does not mean that a species with a greater RGR will have greater growth. *Larix leptolepis*, for example, has a greater RGR than *P. radiata* up until needle fall (Pollard and Wareing, 1968); however *P. radiata* continues to grow after *L. leptolepis* has lost its needles and, in terms of absolute growth, surpasses *L. leptolepis*. Similarly RGR's of *P. radiata* and *P. contorta* are comparable until decreasing daylength causes leaf growth and cambial activity to stop in *P. contorta* (Sweet and Wareing, 1968a) while *P. radiata* is less affected. In a comparison of biomasses with *C. lanceolata*, *P. elliottii* grew faster; this was related to larger leaf area and leaf area index (Liu, 1984). It is possible that a larger leaf area and leaf area index may also be the case for *P. radiata* but this was not measured in this experiment.

C. lanceolata, while not having a true dormancy requirement, nevertheless exhibits a definite seasonal growth pattern terminating with an over wintering bud. *P. radiata* on the other hand has a more adventitious growth habit and under favourable environmental conditions has no inherent dormancy at any season (Florence and Malajczuk, 1970; Cremer, 1973). It is probable that *P. radiata* has a longer growing season because of its ability to resume growth under favourable conditions and hence compensate for its (comparatively) lower RGR. This experiment however can only demonstrate short term growth under such conditions and does not address the issue of duration of growing season. Seasonal growth pattern of *P. radiata* has been studied by Cremer (1973), who found that height growth occurred at all times of the year, when conditions were favourable. Growth was mainly or only in the spring when conditions were adverse. A study of clonal material by Bollmann and Sweet (1976) showed that shoot elongation occurred almost right throughout the year, although at times, elongation was slowed by a reduction in temperature. Rate of elongation was again greatest in spring. As mentioned in the introduction, mean height of *P. radiata* is twice as much as that of *C. lanceolata* at age 25; although this experiment measured biomass rather than height this suggests that a longer growing season may be responsible for greater absolute growth of *P. radiata*.

Temperature: Results showed that most final biomasses were greater for both species at the higher temperature. For *C. lanceolata* this was a similar response to that in the previous temperature experiment and was as expected. It was more surprising to see the

same response in *P. radiata* seedlings as the lower temperature was considered to be better for growth, based on previous work (Hellmers and Rook, 1973).

It is possible that in Hellmers and Rook's studies *P. radiata* seedlings may have been responding to a large day-night differential rather than low (night) temperature *per se*. An increase in biomass would therefore be expected at the higher temperature in this experiment given that the day-night differential was the same as the lower temperature. Height growth was greatest at "high" day temperatures of between 20 and 28 °C (Hellmers and Rook, 1973) and at 30 °C (Florence and Malajczuk, 1970); dry weight was also greatest at 24 °C compared to 30 and 19 °C (Florence and Malajczuk, 1970). The greater growth response of *P. radiata* at 28/13 °C is therefore not inconsistent with other findings, although it must be remembered that there was high mortality of *P. radiata* at this level. Overall performance must consider both growth and survival rates.

In the previous temperature experiment, growth of *C. lanceolata* seedlings was greater at 28/21 °C than 18/11 °C (both 16 hour photoperiod and a 7 °C day-night differential). That final biomass components were significantly different between temperatures in this experiment (with a 13 °C day-night differential) suggests that, in terms of biomass accumulation, *C. lanceolata* responds more to high day temperatures, rather than to night temperature or day-night differentials.

This is partially supported by the RGR's where, in all cases, mean RGR was greater at 28/13 °C than at 20/5 °C (for both species) although the differences were not statistically significant. While mean RGR's were not statistically significant between temperatures for each species, this may have been a result of the experimental design. The experiment was carried out for 42 days; larger differences in RGR may have resulted from a longer growing period. Hellmers and Rook (1973) showed significant differences for *P. radiata* after 3 months.

For *P. radiata* at least the change from nursery to controlled environment conditions would have entailed some transplanting shock and delayed growth. An attempt to minimise this was made by giving seedlings two weeks under glass following uplifting and potting up before the start of the experiment. However observation of roots at harvests and seedling mortality at 28/13 °C suggests that a longer period of acclimatisation was needed, and as a result RGR differences between temperatures would have been masked.

C. lanceolata seedlings, once germinated, were grown in the pots and so were not subject to any transplanting shock at the time of the experiment. Seedlings were considerably larger than *P. radiata* and probably had completed early rapid seedling growth. RGR then may have been slowing down at the time of testing, thus reducing any temperature effect. It was also noted that many seedlings under 20/5 °C developed a winter (red-brown)

colouration of leaves, and began forming terminal buds. This in itself would not necessarily have caused a reduction in RGR of dry weight (Sweet and Wareing, 1968b), but does have implications for height growth (not measured in this experiment).

4.2 Photosynthetic Response

Light response curves: There were unusually high photosynthetic rates at 235/260 μE for C28, C20 and P20 (Table 7.5), these were the first set of readings carried out on the second day of measurements. It is possible that the plants had either not acclimatised to cabinet conditions or that some error in measurement had occurred. This could have occurred in the current set of readings or in the previous set. Regardless of this the overall trends in photosynthetic rates and light saturation between species and temperature treatments are still apparent.

Marked differences were seen between treatments at higher light intensities; C28 had the highest photosynthesis rates at all light levels and was significantly different from all other treatments except at 0/0 and 30/30 μE. C20 was consistently higher than P28 and P20 except at 0/0 μE; P28 and P20 were in general very similar. It appears that overall photosynthesis response was positively related to RGR at a species level and possibly for temperature within species. This is in contrast to the other temperature experiment where provenances with large RGR's had low photosynthetic rates compared to those with low RGR's.

For *P. radiata* temperatures between 20 and 28 ^{o}C do not appear to affect net photosynthesis at the light intensities tested. A similar response was observed by Wood and Brittain (1973), where temperatures of 17, 23, and 29 ^{o}C produced similar light response curves; an optimum temperature of about 23 ^{o}C was suggested. While net photosynthesis was still increasing with light intensity for both temperatures in this experiment, the broad response from 160 to 640 μE indicates that this was approaching light saturation. This may have been due to needle composition; *Pinus taeda* seedlings with primary needles reached maximum photosynthesis at low light intensity whereas older seedlings with developed secondary needles achieved maximum photosynthesis only at full sun light intensities (Kramer and Kozlowski, 1979).

Photosynthesis of *C. lanceolata* was more affected by temperature. For all light intensities other than complete darkness, the difference in photosynthetic rate between temperatures was considerably greater than the difference for *P. radiata*. At the highest light intensities (580/640 μE) there was an increase in photosynthetic rate, from 20 to 28 ^{o}C, of 103.6 % for *C. lanceolata* compared to only 16.2 % for *P. radiata*. Thus *C. lanceolata* over this range of temperature is more sensitive in terms of photosynthesis than *P. radiata*. Although the increase in rate of photosynthesis does not necessarily bring about a corresponding increase in growth (this being also dependant upon leaf

biomass production), in this experiment the increase in growth at the higher temperature can be attributed to the increase in photosynthesis, as leaf biomass was not significantly different between temperatures.

Optimum temperatures for photosynthesis, in general, are similar to daytime temperatures at which the plants normally grow (Salisbury and Ross, 1978); and mean temperatures in July (hottest month) for *C. lanceolata* are 26.9 - 28.6 ^{o}C (Li, pers. comm.). As noted above, this is in contrast to the earlier experiment where photosynthetic rates were higher at lower temperatures. However seedling age differences between experiments probably account for this contrast; the six month old seedlings used in this experiment had fully expanded leaves and therefore relatively stable internal conditions. Thus photosynthesis would be at maximum levels (Schaedle, 1975; Kramer and Kozlowski, 1979). In the previous experiment seedlings were essentially grown from seed and were still undergoing rapid growth as has been discussed.

From Figure 7.3 the broad response curve for *C. lanceolata* seedlings grown at 20 ^{o}C indicate that light saturation was approached and the response curve was similar to those of *P. radiata*. At 28 ^{o}C the *Cunninghamia* response curve was still increasing markedly at the higher light levels; light saturation would be expected to occur at a higher light intensity.

Light Compensation Points: In many species differences in light compensation points are caused primarily by differences in respiration rates (Salisbury and Ross, 1978). The significantly lower light compensation point for *C. lanceolata* suggests that respiration might be less than that of *P. radiata*. However this is not the case as dark respiration at 0 μE is greater, although not significantly so (Table 7.5). The implication therefore is that *C. lanceolata* has greater (gross) photosynthetic efficiency per unit area of leaf. The lower compensation point of *C. lanceolata* was evident in the experiment at 30 μE where *C. lanceolata* was still photosynthesizing (albeit slowly) while *P. radiata* was respiring.

The light compensation point estimate for *P. radiata* at 20 ^{o}C (39.072 μE) was very similar to that obtained by McEwen (1983) of 36.8 μE also at 20 ^{o}C. Seedlings were of a similar size and age; however photosynthesis rates at light saturation were considerably higher in McEwen's study and light saturation itself was well above 640 μE (the upper level in this study).

It is possible that a lower light compensation point may indicate that *C. lanceolata* is less of a pioneer species or adapted to lower light intensities in China. A lower light compensation point means that *C. lanceolata* is able to continue to photosynthesise and accumulate carbohydrates at lower light levels than *P. radiata* (*i.e.* from 39 μE to 20.2 μE). It is therefore a more shade tolerant species. Light curves show approaching light

saturation at 640 μE (full sunlight *ca.* 2000 μE) for *P. radiata* and *C. lanceolata* at 20 °C, but not at 28 °C (for *C. lanceolata*); light saturation levels then do not support this hypothesis as it would be expected that shade tolerant species reach light saturation at lower light intensities (Salisbury and Ross, 1978).

The site preferences of *C. lanceolata* indicate that the species is more of a shade tolerant species, best growth (in China) tends to occur in moist, sheltered and fertile (mesic) conditions which are typical of shade tolerant species (Spurr and Barnes, 1980). However ecologically *C. lanceolata* is probably a early/mid-successional species; in an 80-100 year old mixed evergreen coniferous and deciduous (broadleaved?) forest, data indicated that the *C. lanceolata* community would be succeeded by an evergreen broadleaved community (Fong *et al.*, 1980). While standard plantation practice in China is to plant *C. lanceolata* as a monoculture (*i.e.* in a pioneering species role), evidence from other studies suggests that *C. lanceolata* is adapted to lower light intensities, or at least is less suited to full sunlight. In one study, growth of *C. lanceolata* seedlings was found to be best at 1000 foot-candles compared with 1800 foot-candles and 450 foot-candles (Chiang and Wang, 1982). Similarly when grown in mixed stands with either *Paulownia tomentosa*, *Sassafras tsumu*, or *Pinus massoniana*, growth was higher than those in pure stands (Ni *et al.*, 1983; China, Coop Res Group on Southern Mixed Stands, 1987; China, Mixed Forest Study Group, Fujian, 1979; Du *et al.*, 1988) and photosynthetic intensity was higher in mixed stands with *Paulownia tomentosa* (Ni, *et al.*, 1983). One reason advanced to account for the better performance was the interception of direct solar radiation by the *Paulownia* crowns, thus creating preferred weak sunlight conditions (although other microclimate factors were also improved). *C. lanceolata* is also reported as being used as an understory species in *Araucaria angustifolia* stands in Brazil (Guidoni and Konecsni, 1982). See also chapter II for a complete discussion on mixed stands. In the photoperiod experiment (see chapter XI), growth was not affected by the shading regime; however a visual comparison between full sunlight and 30% shade showed that seedlings grown under shade were a darker green colour and "healthier" in appearance.

5. SUMMARY

Large species differences in growth and photosynthesis were demonstrated in this experiment. Somewhat surprisingly, *C. lanceolata* showed higher relative growth rate than *P. radiata*, regardless of temperature. Similarly, photosynthetic rates were greater for *C. lanceolata*. Growth and photosynthesis of both species were also greater at 28/13 °C than at 20/5 °C.

It would appear that *C. lanceolata* has a faster (physiological) growth rate and more efficient photosynthetic capacity than *P. radiata*, at least at the seedling stage. Absolute

growth rate of a species is determined by the length of the growing season and growth rate during the season. If *C. lanceolata* is a faster growing species under similar growing conditions this would imply that *P. radiata* would have a longer growing season in New Zealand, in order to achieve greater absolute growth, as is evident after 25 years.

The experiment was run for 42 days. In this time *C. lanceolata* seedlings at 20/5 ^{o}C showed formation of terminal buds and winter colouration; probably in response to low night temperature. Growth may have been reduced over a much longer period than the experiment duration; *P. radiata* on the other hand had continuous, steady growth. There were also problems with *P. radiata* seedling acclimatisation to the growth cabinets which may have served to reduce initial growth rate.

Photosynthesis of *C. lanceolata* was more affected by temperature. While *P. radiata* showed no significant differences between temperatures, there was a significant difference for *C. lanceolata.* Photosynthesis was greater at 28/13 ^{o}C than at 20/5 ^{o}C, and this is probably close to the optimum temperature for photosynthesis, corresponding to mean July temperature in China.

Light compensation point was lower for *C. lanceolata* indicating that seedlings can continue to accumulate carbohydrates at lower light intensities than *P. radiata.* It may also indicate that *C. lanceolata* is less suited to high light intensities and therefore not as much of a pioneer species as *P. radiata.*

Table 7.1: Mean RGR Values -a) by Species; b) by Treatments

	RGR (g g^{-1} day^{-1})			
	lnT	lnS	lnR	lnL
a) Species				
C. lanceolata	0.02681 [a]	0.03074 [a]	0.02911 [a]	0.02487 [a]
P. radiata	0.01365 [b]	0.01867 [b]	0.02132 [b]	0.01056 [b]
R^2	0.840342	0.739339	0.857332	0.832238
b) Treatments				
C28	0.030055 [a]	0.034212 [a]	0.035746 [a]	0.026543 [a]
C20	0.023567 [ab]	0.027267 [ab]	0.022467 [ab]	0.023200 [ab]
P28	0.017091 [bc]	0.021474 [bc]	0.024574 [ab]	0.014103 [bc]
P20	0.011551 [bc]	0.016885 [bc]	0.019281 [b]	0.008446 [c]
R^2	0.846487	0.745629	0.866572	0.836390

values in the same column with the same letter are not significantly different at the 95% level.

Table 7.2: Mean Final Growth Measures - Biomass Components (g)

Variable	T	S	R	L
C28	11.705 [a]	1.726 [a]	3.301 [a]	6.678 [a]
C20	9.593 [b]	1.373 [b]	2.182 [b]	6.038 [a]

values in the same column with the same letter are not significantly different at the 95% level.

P28	3.186 [a]	0.6211 [a]	0.5623 [a]	2.002 [a]
P20	2.507 [b]	0.5292 [a]	0.3905 [b]	1.588 [b]

values in the same column with the same letter are not significantly different at the 95% level.

Table 7.3: Probability (Pr > F) Values For Effect of Temperature Treatment on Final Growth Variables

Variable:	T	S	R	L
C. lanceolata	0.0090	0.0184	0.0068	0.1172
P. radiata	0.0136	0.1168	0.0307	0.0156

Variable:	S:R	S:L	S:T	R:L	R:T	L:T
SP	0.0001	0.0001	0.0001	0.0001	0.0001	0.0303
TR	0.5269	0.6431	0.6249	0.0299	0.0358	0.0234
SP x TR	0.9840	0.0425	0.2250	0.1289	0.2058	0.0299

Table 7.4: Mean Final Growth Measures - Derived Ratios

Variable:	S:R	S:L	S:T	R:L	R:T	L:T
Species:						
P. radiata	1.385 [a]	0.3266 [a]	0.2063 [a]	0.2580 [a]	0.1617 [a]	0.6323 [a]
C. lanceolata	0.608 [b]	0.2421 [b]	0.1452 [b]	0.4295 [b]	0.2512 [b]	0.6038 [b]
Temperature:						
28 °C	0.853 [a]	0.2786 [a]	0.1665 [a]	0.4173 [a]	0.2381 [a]	0.5956 [a]
20 °C	1.029 [a]	0.2801 [a]	0.1767 [a]	0.3033 [b]	0.1908 [b]	0.6328 [b]
SP x TR:						
P28		0.3137 [a b]				0.6314 [a]
P20		0.3342 [a]				0.6328 [a]
C28		0.2582 [b c]				0.5747 [b]
C20		0.2260 [c]				0.6328 [a]

values in the same column with the same letter are not significantly different at the 95% level.

Table 7.5: Mean Net Photosynthesis (μmol m^{-2} s^{-1}) at Different Light Levels (μE)

Light (μE):	580/640	345/360	235/260	160/160	50/55	30/30	0/0
Species:							
C. lanceolata	7.037 a	5.024 a	5.833 a	3.895 a	1.530 a	0.438 a	-0.676
P. radiata	2.750 b	1.475 b	1.869 b	1.144 b	0.006 b	-0.240 b	-0.432
Temperature:							
28 °C	6.196 a	4.001 a	3.959	2.855	1.036 a	0.222	-0.593
20 °C	3.591 b	2.499 b	3.744	2.185	0.500 b	-0.024	-0.516
SP x TP:							
C28	9.437 a	6.513 a	6.829 a	4.890 a	2.008 a	0.641	-0.705
C20	4.636 b	3.535 b	4.837 ab	2.900 b	1.053 b	0.234	-0.648
P28	2.955 b	1.488 c	1.088 c	0.819 c	0.065 c	-0.198	-0.481
P20	2.546 b	1.462 c	2.650 bc	1.469 bc	-0.053 c	-0.283	-0.384

values in the same column with the same letter or no letters are not significantly different at the 95% level.

Table 7.6: Probability (Pr > F) Values For Photosynthesis

Light (μE)	Species (SP)	Temperature (TR)	SP x TR
580/640	0.0003	0.0112	0.0267
345/360	0.0001	0.0011	0.0013
235/260	0.0001	0.6855	0.0050
160/160	0.0001	0.1436	0.0095
50/55	0.0001	0.0108	0.0366
30/30	0.0100	0.2891	0.4821
0/0	0.0501	0.5054	0.8607

Table 7.7: Light Compensation Points (μE)

Species: p = 0.0032		SP x TR: p = 0.1065	
P. radiata	49.598	P28	57.492
C. lanceolata	20.246	P20	39.072
Temperature: p = 0.4944		C28	16.318
28 °C	36.905	C20	24.173
20 °C	30.559		

Figure 7.1: Relative Growth by Species

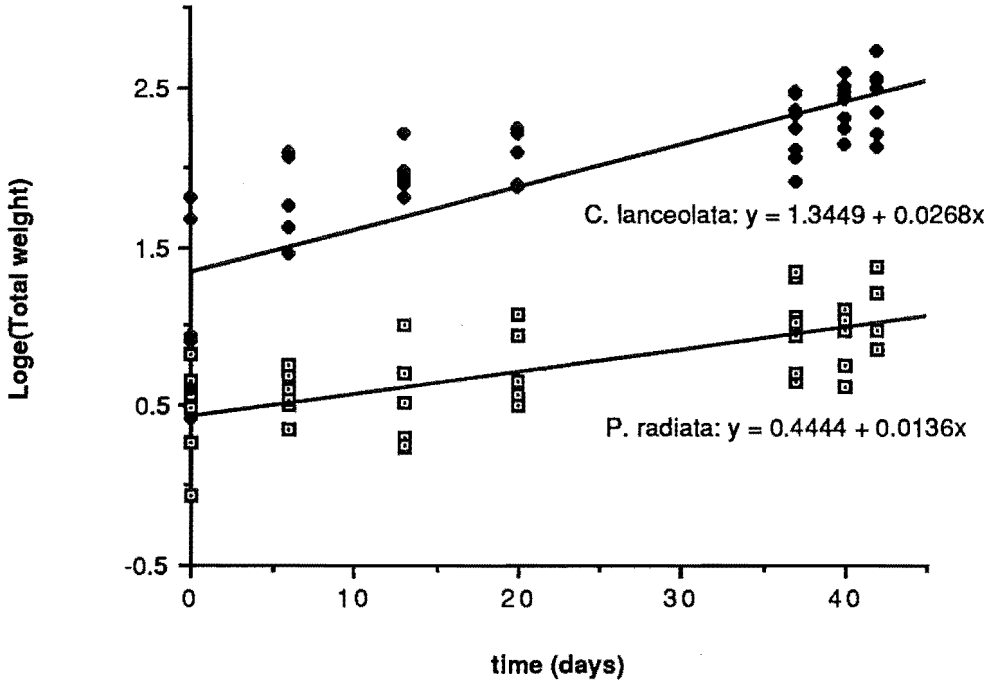


Figure 7.2: Relative Growth Rate by Species and Temperature

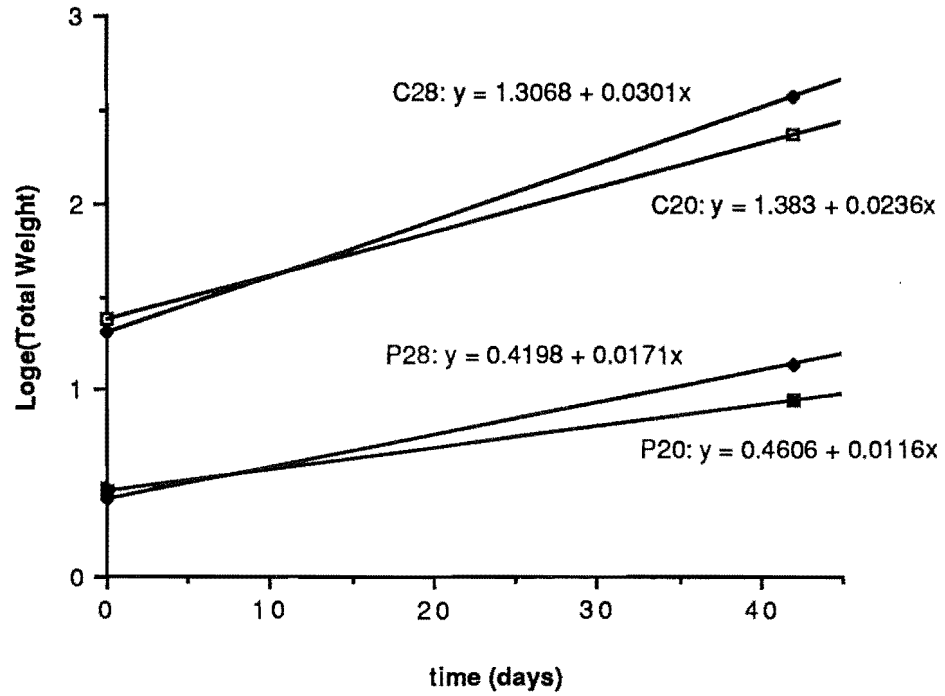
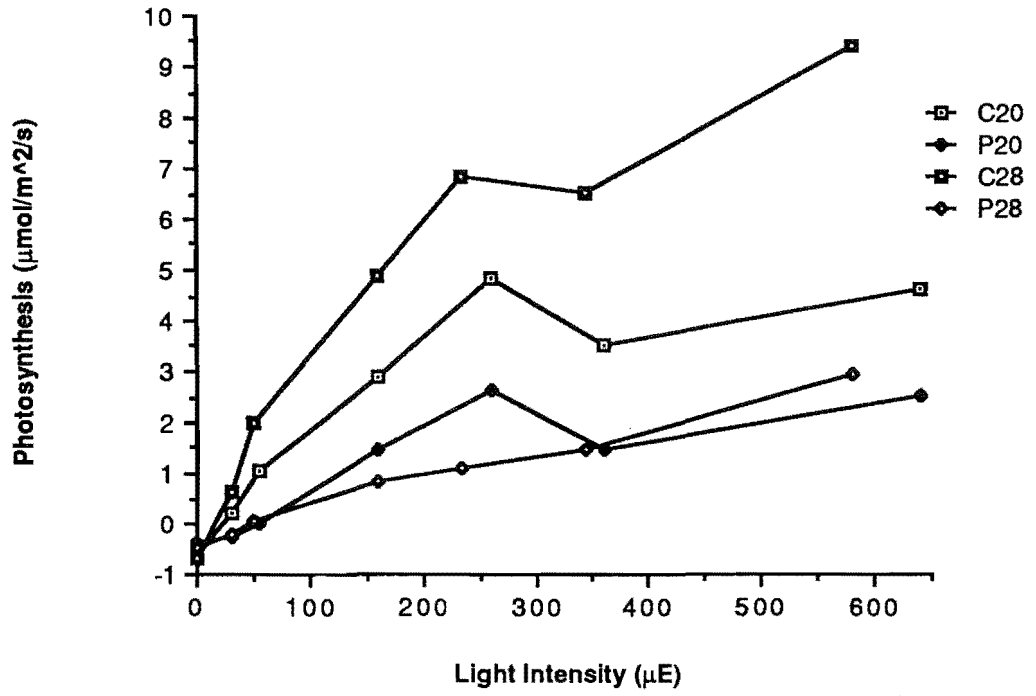


Figure 7.3: Photosynthesis by Species and Temperature



CHAPTER VIII

FROST RESISTANCE OF SEEDLINGS

1. INTRODUCTION

Successful introduction of a species into a new locality depends on a number of factors. Frost resistance can be an important factor, especially when the new locality is cooler than the species' native climate. The northern limit of many woody species is determined by the lowest temperature they can survive (Kramer and Kozlowski, 1979); and in China the northernmost limit of *C. lanceolata* corresponds closely to the 0 ^{o}C January isotherm which lies mainly along latitude 33 ^{o}N (Watts, 1969). The main production area follows 6 - 10 ^{o}C January isotherm (FAO, 1982), thus there is a wide range of winter temperatures within *C. lanceolata*'s distribution.

Frost can be a problem when establishing species in temperate regions (Menzies *et al.*, 1987), especially subtropical plants. Failure of a species at establishment can often be attributed to harsh environmental conditions such as frosting (Lundmark and Hällgren, 1987), however frosts are usually only a problem in the first few years of establishment (Menzies *et al.*, 1987), presumably until tree growth is above the frosting level. In some cases amelioration of site conditions (*e.g.* weeding, site preparation, shading) can overcome frost problems (Menzies *et al.*, 1987; Lundmark and Hällgren, 1987) although this may not be practical in all cases and on a large scale.

Assessing a species' frost resistance can provide information on it's suitability to a new site; furthermore if provenance or other genetic variation is present selection of provenances or genetically suitable lines can be made according to site conditions. With such a wide range of winter temperatures it is possible that *C. lanceolata* may exhibit provenance variation in frost resistance; there is reported variability in the Chinese literature (see chapter III).

Frost resistance follows a seasonal pattern (Flint, 1972; Kramer and Kozlowski, 1979; Menzies *et al.*, 1981; Tibbits and Reid, 1987) which is closely related to growth patterns. In most studies mid winter frost resistance is assessed as this gives an indication of maximum frost resistance. In cold-hardy tree species hardening is controlled by sequential changes in day length and temperature (Weiser, 1970; Greer, 1983); a full description is given in section 4.2. Phenology is often related to cold hardiness;

provenances of *Pseudotsuga menziesii* with earlier bud set were less susceptible to early frosts (Kramer and Kozlowski, 1979).

Rate of dehardening is more dependant upon temperature, although photoperiod may have an effect on timing of induction of dehardening (Greer and Stanley, 1985). It appears that dehardening in some Chinese tree species may occur earlier or faster than more northern species; Dallimore and Jackson (1931) have noted that a number of (Chinese) species planted at Kew, England suffer from early autumn or spring frosts (*e.g. Keteleeria spp., Larix dahurica, L. potaninii*). Others have been unable to withstand severe winters (*C. lanceolata*) or are restricted to mild areas of Britain (*e.g. Fokienia, Glyptostrobus, Libocedrus macrolepis*). This may be a result of tight adaptation to native environment where there is little variation in winter and summer temperatures (see chapter III) and hence susceptibility to out of season frost is increased. Frost damage to tips of seedlings were seen in the nursery trial in both autumn and spring (chapter IV) indicating that this is the case with *C. lanceolata.*

Two experiments were carried out to assess frost resistance. In the first, mid-winter resistance on one-year-old seedlings from a number of provenances was measured to gain an idea of maximum frost levels the species can tolerate, and to assess any provenance variation. The second experiment was designed to test susceptibility of soft tissue to out of season frost.

2. MATERIALS AND METHODS (Winter Frost Resistance)

One-year-old seedlings from thinnings of the nursery trial at the University of Canterbury (see chapter IV) were used in the experiment. Seedlings were lifted from the nursery beds over 10 - 12 July 1989 and potted into plastic planter bags (PB $1^1/_2$'s) with commercial potting mix and 3-month "Osmocote" fertiliser. Seedlings were then placed in a glasshouse to minimise transplanting shock before transport to Palmerston North.

Seedlings were then transported on 15 July by van to the Plant Physiology Division, DSIR, Palmerston North. They were repotted into 12 cm (height) x 15 cm (diameter) pots, blocked by height (two blocks) and placed outside in a sheltered area. Seedlings were then subjected to three frost temperatures over a period of three nights (17 - 19 July). Frosting was carried out in two low temperature controlled environment rooms (representing the blocks), previously described by Robotham et al. (1978).

After frosting the seedlings were transported back down to Canterbury and placed in a glasshouse heated to 10 ^{o}C and visually assessed for damage at eight weeks after frosting. Assessment was as per Menzies (1977).

2.1 Provenance Material

Provenances (PV) were as follows:

PV:	1	2	3	4	5	7	8	9	10	11	12
Nos. seedlings:	40	35	35	35	25	8	8	40	40	30	12

Except for PV's 7, 8 and 12 seedling numbers for each frost were between four and six seedlings per block. PV's 7, 8 and 12 were only tested in the lightest frost treatment (- 8 ^{o}C) due to low seedling numbers.

2.2 Treatment Conditions

Frosting conditions were as follows:

Treatment	Min Temp (^{o}C)	Programme (Freeze-Duration-Thaw)
1	- 8	6-6-4 (hours)
2	-12	6-6-4
3	-15	6-6-4

The frost programme of 6-6-4 used is the standard programme run by the Plant Physiology Division; differences in freezing and thawing rates between treatments are not considered to affect damage results (Warrington and Jackson, 1981). Test runs were not carried out as previous work by Sakai (1971) found that *C. lanceolata* twigs did not withstand freezing below 13 ^{o}C (see section 4.2). The coldest frost level was considered an appropriate level at which significant damage would occur.

Seedlings were randomly arranged in insulated trays in the frost rooms at 10 ^{o}C for an hour before temperatures were decreased. Relative humidity during the minimum temperature duration was 100 %, and approximately 40 % at 10 ^{o}C. Soil temperature during frosting was maintained at 5 ^{o}C by heating elements in the trays.

Frosting runs were carried out in darkness except for the last hour of the thawing cycle when lights were turned on. Actual frost temperatures varied slightly from desired temperatures and were as follows:

	Treatment		
	1	2	3
Room 1	-8.4	-12.4	-15.3
Room 2	-8.1	-12.0	-14.9
(Average	-8.2	-12.2	-15.1)

A fourth frosting temperature of -18 ^{o}C was carried out on spare seedlings one week after the other runs. Three seedlings each from provenances 2-4 and 9-11 were used in one run only.

2.3 Measurements

Following frosting, plants were left for eight weeks and then visually graded. Grading was as given by Menzies (1977), each seedling was graded according to frost damage as follows:

Grade	Damage
0	no damage
1	some leaves slightly damaged
2	10 - 30% of leaves killed
3	50% of leaves killed
4	90% of leaves killed
5	seedling dead

Within each block scores for seedlings were averaged by PV. Mean scores for each PV were then plotted against temperature, and frost hardiness (H) values were obtained by interpolation or conservative extrapolation. Overall H was also estimated by plotting overall mean scores against temperature.

2. 4 Analysis

Frost scores were analysed as a two factorial design. The analysis of variance (ANOVA) format was :

Source	df	
	design	actual
Blocks (runs)	1	1
Frost (TR)	2	3
Provenance (PV)	10	10
TR x PV	20	19
Error	32	26
TOTAL	65	59

As not all provenances were represented in all frost treatments, the general linear model (GLM) procedure was used to account for the unbalanced design.

3. RESULTS

3.1 Frost Damage

Highly significant differences were apparent between frost temperatures ($p = 0.0001$); overall damage was greater at lower temperatures of -15 and -18 °C, there was no significant difference between the -8 and -12 °C frosts. Significant differences were also apparent between provenances ($p = 0.0469$) with PV 4 showing the greatest overall damage and PV 1 showing the least (over three frost temperatures). Table 8.1 shows mean frost damage scores for all provenances.

There was no significant frost x provenance interaction or difference between rooms (blocks) despite the slight variation in frost temperatures between rooms.

Overall, damage was negligible in the -8 and -12 °C frosts; the exception to this was PV 11 which had an unusually high percentage of seedlings severely damaged (damage score of 3 or greater). At -15 °C typically 20 % or more seedlings were severely damaged while at -18 °C all but two seedlings were severely damaged (usually dead). The percentage of severely damaged seedlings are shown in Table 8.2. Typical seedling appearance after frosting is shown in Plate 8.1, and detail of frost damage at -15 °C is shown in Plate 8.2.

3.2 Frost Hardiness

Frost hardiness (H) was assessed as the level of frosting seedlings could tolerate with a damage score of 2 (Menzies and Holden, 1981; Greer and Warrington, 1982). This arbitrary (and conservative) level of frost temperature has been used consistently for frosting studies carried out on *Pinus radiata* at the DSIR, and so is adopted for this experiment.

Means of scores for each provenance and for the species overall were plotted against the frost temperatures. Conservative estimation by linear interpolation was used to determine H where mean damage scores exceeded 2. For PV 1 where the mean damage score did not exceed 2 at -15 °C, conservative extrapolation was used to estimate H. An exponential curve was fitted to overall mean damage scores. Figures 8.1 - 8.3 show mean damage against frost temperatures, H estimates are shown in Table 8.2.

4. DISCUSSION

4.1 Provenance Differences

Three provenances, PV's 7, 8 and 12, were only represented in the lightest frost treatment. As this treatment failed to produce any significant damage these provenances (unless specifically referred to) will be omitted from the following discussion. Overall H for *C. lanceolata* as a species appears to be around -15.5 ^{o}C using linear interpolation between scores at -15 and -18 ^{o}C. If the fitted exponential curve in Figure 8.3 is used (Score = $0.0113 * 10^{(0.141*\text{Frost Temp})}$) then H increases to -15.9 ^{o}C.

As can be seen from Table 8.2, H values varied only between -15.0 and -16.0 ^{o}C for all provenances except PV 4 which had an H value of -13.7 ^{o}C. This is consistent with the damage scores which indicate that PV 4 had the greatest overall damage, although this damage was only statistically significantly different from PV 1.

While results were otherwise not significantly different, two provenances did appear to suffer more damage then the others; PV's 4 and 11 between -12 and -15 ^{o}C had greater mean damage scores (Table 8.1) then most others (except PV 5 at -15 ^{o}C). This was also apparent in the number of severely damaged seedlings at -15 ^{o}C (Table 8.2). However the slight provenance variation in frost tolerance does not seem to be related to environmental parameters such as latitude, longitude, or altitude. This contrasts with Chinese experience which identified Nanling provenances (PV's 1 - 5, 11 , 12) as those with the best frost resistance (China, National Collaborative Research Group on Provenance Trial of Chinese Fir, 1988; see also chapter III).

Provenance variation in frost tolerance has been reported in other species such as *Quercus rubra* (Flint, 1972), *Eucalyptus nitens* (Tibbits and Reid, 1987), *E. regnans* (Rook et al., 1980) and *Pseudotsuga menziesii* (Kramer and Kozlowski, 1979). Genetic variation in *Pinus radiata* and *P. sylvestris* has also been documented (Menzies et al., 1987; Nilsson and Andersson, 1987) although differences were found between clones of *P. sylvestris* this was not related to latitude of origin (Nilsson and Andersson, 1987). Tolerance for many species appears to be, at least in part, related to minimum site temperatures (Tibbits and Reid, 1987) or altitude and latitude (Pollock et al., 1986; Flint, 1972) which tend to be closely correlated with minimum temperatures and frost free period (Flint, 1972).

Minimum temperatures and frost free periods reported for *C. lanceolata* provenances are given in Table 8.3. However, as before, there does not appear to be any close relationship between frost tolerance and the above climate data: PV4 and PV1 have similar mean January temperatures, and while there are more frost free days at PV4's site there is no trend with other PV's. It is reasonable to assume from these results that there

is some provenance variation in frost tolerance for *C. lanceolata*, but that this appears to be unrelated to the climate factors considered.

Unfortunately, due to absence of stand histories and details it is not possible to ascertain the validity of regarding the seedlots used here as true provenances. Given the long plantation history of *C. lanceolata*, it may be that seed exchange between areas has resulted in less variability between areas then there would have been in natural provenances. Provenance differences are not always apparent; Kramer and Kozlowski (1979) reported that no differences were found between provenances of *Populus deltoides* and *Salix nigra* or 21 clones (from different geographic locations) of *Cornus stolonifora.*

Variation in frost tolerance was clinal for *Q. rubra* and ecotypic differences in species are usually associated with differences in growth rate or time of cessation of growth (Flint,1972). The one year old nursery seedlings used in this experiment did not show large differences in either of these factors (pers. observation) and is consistent with the frost results. Timing of cessation of growth was apparent in the second year so it is possible that some variation may exist (see chapter IV). Phenology was not found to be important in selection of frost resistance for *P. radiata* (Menzies *et al.*, 1987) and although dormancy is associated with development of frost resistance, Weiser (1970) concluded that cessation of growth (rather than dormancy) was the major factor in induction of hardiness. Dormancy in many temperate species may be in effect well before development of hardiness and southern (US) pines when in a dormant phase did not tolerate low temperatures (Kramer and Kozlowski, 1979).

4.2 Frost Tolerance Requirements

As mentioned above H is approximately 15.5 to 15.9 for *C. lanceolata* as a whole. This finding is in contrast to that of Sakai (1971) who found that twigs of *C. lanceolata* did not withstand freezing below -13 ^{o}C. The discrepancy may be explained by several factors. Firstly twigs used were artificially hardened before freezing, and secondly twigs were obtained from 40 year old trees as opposed to one-year-old seedlings used in this experiment. Determination of freezing resistance differs slightly from the method adopted here although results are generally comparable (D. Greer, pers. comm.; Hawkins, 1989).

Frost hardening of the seedlings was allowed to occur naturally. Although the hardening requirements for *C. lanceolata* are not specifically known it is generally assumed that frost tolerance for species is greatest in mid winter (Pollock *et al.*, 1986; Greer, 1983). The hardening process is thought to occur in two or three phases as proposed by Weiser (1970); the first being largely induced by shortening photoperiod (Greer, 1989), later low temperatures below a threshold temperature (5 ^{o}C for *P. radiata*) control hardening

(Greer, 1983). Subsequent exposure to moderate frosts can further increase hardiness (Greer and Warrington, 1982).

As the experiment was carried out in mid-late July seedlings would have been close to maximum hardiness if *C. lanceolata* followed similar patterns of development. Seasonal dehardening may have occurred shortly after the winter solstice (21 June, 1989), almost one month prior to the experiment. However low temperatures around this period would have been more important in affecting the rate of dehardening (Greer and Stanley, 1985); *P. radiata* seedlings deharden at temperatures above a threshold of around 6.5 ^{o}C. In addition it may be questioned if photoperiod, while influencing *P. radiata* and other temperate species, has a significant effect on sub-tropical species such as *C. lanceolata.* So even if dehardening was initiated by increasing daylength, low temperatures (below the threshold) would produce a minimal or zero dehardening rate.

A previous experiment indicated that there was no difference in growth response by *C. lanceolata* to different photoperiods (see chapter XI). This is not unexpected given that seasonal differences in photoperiod are relatively smaller in sub-tropical areas than temperate areas. What bearing this has on frost hardening and dehardening is not known at this stage, but evidence from other species reported in Greer and Stanley (1985) suggest that this is likely to be unimportant.

Comparisons of frost hardiness with New Zealand native species and New Zealand grown *P. radiata* show that *C. lanceolata* has a relatively high degree of frost hardiness. Native podocarps have frost hardiness temperatures of -4.1 to -9.7 ^{o}C (Hawkins, 1989) while *P. radiata* has maximum winter frost hardiness of about -12 to -14 ^{o}C. *C. lanceolata* then should be able to withstand most New Zealand winter conditions with respect to frost damage. Specimen trees privately grown from cuttings and several years old (up to 2 m) have been reported to withstand 8 ^{o}C frosts in Frankton (Mortimer, 1987).

While New Zealand winter frosts in other than alpine sites are unlikely to *frequently* drop below -15 ^{o}C, it should also be noted that nursery / growing site has an important bearing on frost hardiness. Clear differences between lowland, coastal and high-altitude, inland sites have been demonstrated by Menzies *et al.* (1981). Thus while results for seedlings raised in Canterbury indicate high frost hardiness, this may well be reduced if seedlings were raised in milder environments less subject to winter frostings.

Furthermore, cultural practices such as shading may also affect resistance by directly influencing temperature and indirectly reducing photoinhibition and subsequent photooxidation, as has been reported for *Picea abies* and *Pinus sylvestris* (Lundmark and Hällgren, 1987). In China silvicultural practices have shown the benefits of using a nurse species (to reduce ice damage) for *C. lanceolata* (see chapter II) and shading in this

study (chapter XI) has also produced healthier looking seedlings. It is possible that some form of shading would be useful in reducing frost damage for *C. lanceolata*, although this in turn may affect hardening rates.

4.3 Evolution Pattern and Frost Tolerance

Cunninghamia has been previously described as a member of the "Arcto-Tertiary flora" that evolved in the Arctic during the Cretaceous period and dominated during the Tertiary (Sakai, 1971). See also chapter V, section 4.2. The concept is useful in visualising the extent of *Cunninghamia* s widespread distribution during this period when the climate was warmer then at present. Towards the end of the Tertiary when cooling of the climate began to occur *Cunninghamia* species disappeared from North America and *C. lanceolata* was completely eliminated from Japan (Tanai, 1972), indicating that *Cunninghamia* can be considered as climatic relict species. This suggests that cool climatic conditions such as frost tolerance and/or winter desiccation may be important factor(s) limiting the northern boundaries of *C. lanceolata* 's present day distribution (Sakai, 1971).

If it is likely that frost tolerance is limiting, this may be an important factor when considering introducing *C. lanceolata* to new locations. For New Zealand conditions winter damage by frosts is unlikely to seriously affect survival; however seasonal frost tolerance patterns may be more important, and as a climatic relict from a more uniform and warmer period it may be more susceptible to unseasonal frosts in spring or autumn.

5. MATERIAL AND METHODS (Dormant/Active Frost Resistance)

Methodology and analysis are similar to that of the mid-winter frost experiment. The experiment was carried out in winter between 29 July and 2 August 1991.

5.1 Material

Seedlings were selected for uniformity of height, but randomly selected from various provenances. Provenance differences were assumed to be minimal from the previous winter frost resistance experiment. However, provenance differences may be more apparent in timing of resumption and cessation of growth (see chapter IV) rather than hardiness of active (soft) tissue. Provenance differences in frost resistance are more apparent over mid winter than any other time for *Eucalyptus nitens* (Tibbits and Reid, 1987), a similar situation was seen in *Quercus rubra* (Flint, 1972). This reflects differences in mid winter temperatures between geographic locations and the (relative) uniformity resistance of active tissue regardless of location.

Two year old seedlings in three conditions were used:

i. Dehardened, actively growing.
ii. Naturally hardened, green colouration.
iii. Naturally hardened, brown winter colouration.

Dehardened seedlings were placed in a growth cabinet under high day/night temperatures (28/13 ^{o}C) and long daylength (16 hours). High temperatures are known to increase the rate of dehardening (Greer and Stanley, 1985) and the aim was to obtain seedlings that had just resumed growth following winter dormancy. After four weeks seedlings had lost their brown winter colouration and showed signs of bud swelling or burst. Seedlings were then transferred to a heated (*ca.* 20 ^{o}C) glasshouse for two weeks prior to testing.

5.2 Treatment Conditions

Five seedlings from each condition were frosted at two temperature levels: -5 ^{o}C and -10 ^{o}C. Frosting conditions were as follows:

Treatment	Min Temp (^{o}C)	Programme (Freeze-Duration-Thaw)
1	- 5	6-6-4 (hours)
2	-10	6-6-4

Dehardened seedlings were kept under cover before and after frostings in order to prevent further (natural) frosting.

6. RESULTS AND DISCUSSION

Results were evident after one week and clearly showed differences between hardened and dehardened plants. Dehardened seedlings were all completely killed at both -5 and -10 ^{o}C frosts while both sets of hardened seedlings (green or brown colouration) were completely unharmed. Statistical analysis was therefore redundant.

For the hardened seedlings, the results while only using a small number of seedlings, are in agreement with the earlier mid-winter frost tests which showed negligible damage to seedlings of most provenances at -8 and -12 ^{o}C. If there is any difference in frost hardiness between green and brown coloured seedlings that have been hardened, it is not apparent at either -5 or -10 ^{o}C, and presumably it would occur at lower frost temperatures.

Dehardened seedlings were subjected to over severe frosts; unfortunately it was not possible to use lighter (0 to -4 °C) frosts as the experiment was carried out in conjunction with other (unrelated) studies. In natural growing conditions *C. lanceolata* resumes growth in spring, bud burst occurs around late September - early October (see chapter IV). At this stage and throughout summer, seedlings are in an actively growing and dehardened state; frost damage in this period would adversely affect growth and survival depending on frost severity. In the nursery experiment, frost damage was found to occur in the week following early autumn frosts of -0.5 to -3.5 °C (towards the end of the growing season).

Phenology then, can have an important bearing on resistance to autumn and spring frosts (Kramer and Kozlowski,1979; Flint, 1972). For *P. radiata* this was subordinate to year-round differences (Menzies *et al.*, 1987) but this was most likely due to it's growth pattern. Evidence from Dallimore and Jackson (1931) suggests that Chinese species, including *C. lanceolata*, are more likely to suffer frost damage at these times rather than in mid winter when maximum frost resistance has been obtained.

Chinese climate data for *C. lanceolata* shows that temperatures do not fall below 0 °C between April and October for northern provenances and March and November for southern provenances (Watts, 1962). In the absence of frost, resumption of growth would occur early in this period, and similarly cessation of growth would occur late. Transferring the species to a more variable climate, such as New Zealand, where frosts can occur within the growing season would then result in increased likelihood of frost damage. The results from the second year of the nursery trial illustrate this and are discussed more fully in that chapter. Thus while there was little provenance variation in mid-winter frost resistance, early spring and late autumn frosts are of more importance in provenance selection for New Zealand conditions. Late flushing and early bud setting provenances are more likely to avoid such frosts and in this respect northern provenances with shorter growing seasons would appear to be more suitable.

7. SUMMARY

In terms of New Zealand winter conditions *C. lanceolata* has a high frost resistance (although differences in frost resistance may arise in different nursery sites). *C. lanceolata* can withstand heavier frosts than some native Podocarps and is slightly more hardy than *P. radiata*. Differences between provenances are mostly not significant, other than between PV 4 (least hardy) and PV 1 (most hardy); there is no readily apparent reason for this difference. As a species *C. lanceolata* is frost hardy to about -15.5 to -15.9 °C.

Out of season frosts are likely to cause damage to *C. lanceolata* than mid-winter frosts, reflecting the species' adaptation to a climate where these frosts are very rare. Provenance variation would be expected to be minimal, as differences are usually greatest during mid-winter and least during mid-summer. However phenology may be important in terms of resistance to autumn and/or spring frosts; and thus the timing of cessation and resumption of growth and associated hardening and dehardening would be more important to the successful establishment of *C. lanceolata* in New Zealand than mid-winter frost resistance.

Table 8.1: Frost Tolerance; Mean Damage Scores of Provenances By Frosts

	-8 °C	-12 °C	-15 °C	-18 °C	Overall
PV1	0.083 g	0.333 g	1.250 efg	-	0.556 bc
PV2	0.000 g	0.300 g	1.200 efg	4.000 abc	0.818 abc
PV3	0.000 g	0.500 fg	1.200 efg	3.333 bc	0.818 abc
PV 4	0.125 g	1.000 efg	2.750 cd	5.000 a	1.704 a
PV 5	0.125 g	0.250 g	2.000 de	-	0.792 abc
PV 7	0.000 g	-	-	-	0.000 c
PV 8	0.625 efg	-	-	-	0.625 bc
PV 9	0.600 efg	0.600 efg	0.900 efg	4.333 ab	1.030 ab
PV10	0.083 g	0.083 g	1.417 defg	3.667 abc	0.769 abc
PV11	0.111 g	1.333 efg	1.900 def	5.000 a	1.400 ab
PV12	0.000 g	-	-	-	0.000 c
All	0.163 c	0.519 c	1.525 b	4.176 a	

Damage scores: 0 = no damage 1 = slight damage 2 = 10 - 30 % leaves killed
3 = 50 % leaves killed 4 = 90 % leaves killed 5 = seedling dead.

Values with same letter are not significantly different at the 95% level. Letters in Overall column and All row are for separate analyses and apply only to that row/column.

Table 8.2: Percentage of Seedlings Scoring 3 or Greater and Frost Hardiness Estimates, H (italics indicates extrapolated value)

	-8 °C	-12 °C	-15 °C	-18 °C	H
PV1	0.00	0.00	16.66	-	*15.9*
PV2	0.00	10.00	20.00	66.67	15.9
PV3	0.00	10.00	10.00	100.00	16.1
PV4	0.00	10.00	50.00	100.00	13.7
PV5	0.00	0.00	37.50	-	15.0
PV7	0.00	-	-	-	-
PV8	12.50	-	-	-	-
PV9	10.00	10.00	20.00	100.00	16.0
PV10	0.00	0.00	25.00	66.67	15.8
PV11	0.00	44.44	50.00	100.00	15.1
PV12	0.00	-	-	-	-
All	2.02	9.88	21.95	88.23	15.5

Table 8.3: Winter Temperatures, Frost Free Days and Days Above 10 °C For Provenance Material

	Temperature (°C)		Days	Days
	Mean Jan.	Abs. Min.	> 0 °C	> 10 °C
PV1	9.2		235	
PV2, 11, 12	9.2		283	
PV3	8.0		290	
PV4	9.1		297	
PV5	4.9		280	
PV7	6.5	-8.4*	234	258*
PV8	2.1*	-10.1*		220*
PV9	2.9	-15.3*	200	222*
PV10	1.9	-13.8**	202	

(from Li, pers. comm.; * from Wu, 1984; and ** from Watts, 1969)

Figure 8.1: Frost Damage for PV's 1 - 4

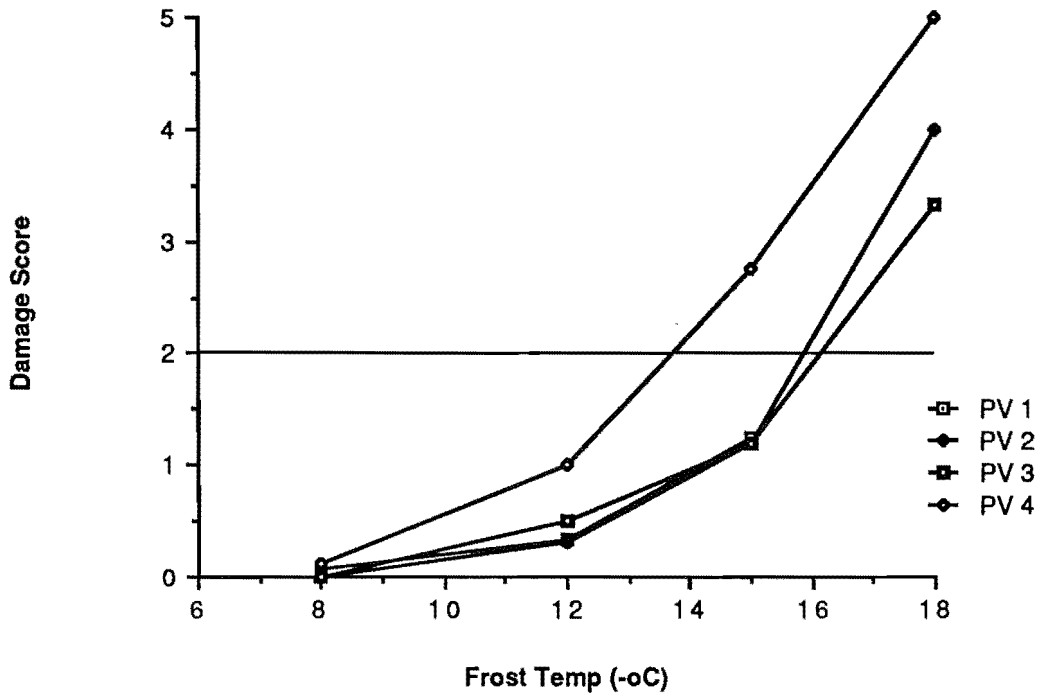


Figure 8.2: Frost Damage for PV's 5, 9 - 11

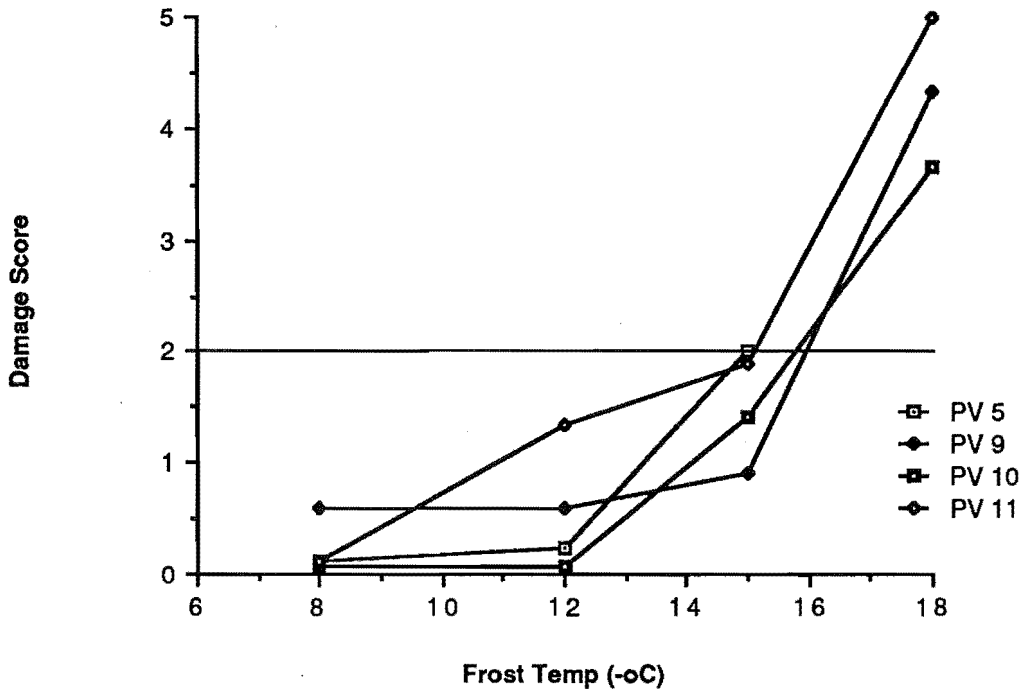


Figure 8.3: Mean Damage Scores (All PV's)

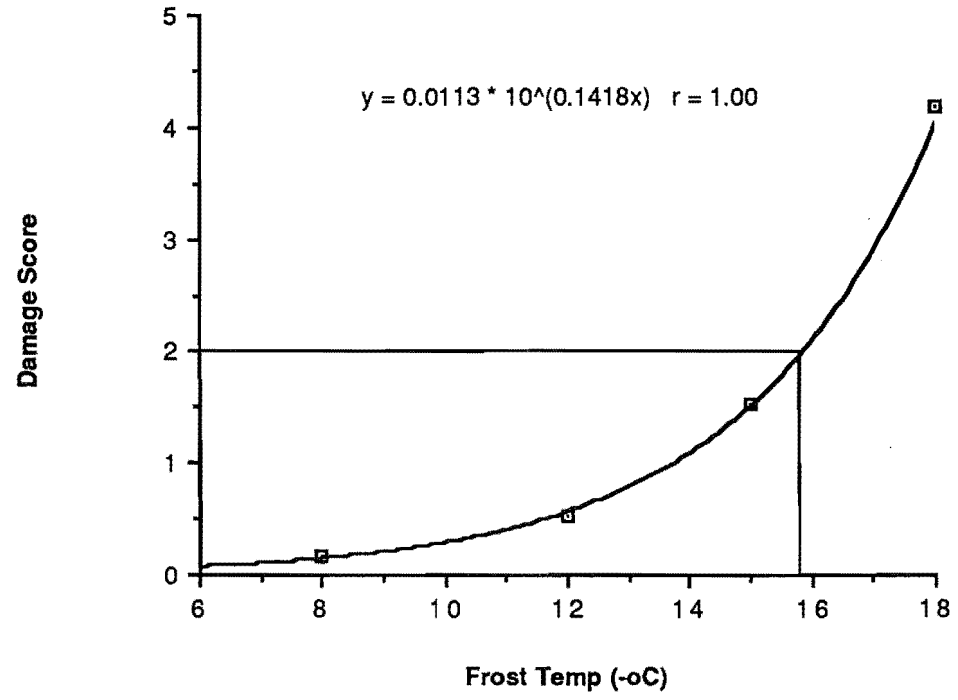


Plate 8.1: Seedling Damage Response to Several Frost Temperatures

(From left to right: PV4, -15 °C; -12 °C; -8 °C; PV1, -8 °C)

Plate 8.2: Detail of Frost Damage at -15 °C, PV4

CHAPTER IX

GROWTH OF SEEDLINGS UNDER DIFFERENT WATER STRESS LEVELS

1. INTRODUCTION

Water stress is one of the most important factors affecting tree growth, survival and distribution (Kramer, 1983; Seiler and Johnson, 1985); and within a species' distribution, productivity is closely related to available water (Salisbury and Ross, 1978). The importance of water to plant life is due to its role in plant functions: Water forms 80 - 90 % of the fresh weight of tissue; is the solvent in which cell transport operates; it is a reagent in photosynthesis, and; is essential for maintaining turgidity (Kramer and Kozlowski, 1979). When water becomes limiting, disruption to these plant functions can occur. Newly planted seedlings can often develop severe water deficits and are sensitive to stress due to small root systems (Seiler and Johnson, 1985).

Provenance tests of *Pinus taeda* indicate that provenances from drier climates have greater drought resistance, possibly as a result of more extensive root systems and rapid reductions in leaf conductance as soil moisture is depleted (Bongarten and Teskey, 1986). Similar responses have been reported for other conifer species; *P. radiata* and *Pseudotsuga menziesii* in Teskey *et al.* (1987). In the case of both *Pinus taeda* and *Pseudotsuga menziesii* the native ranges of the species have a wide range of moisture conditions. *C. lanceolata* has a wide mean annual rainfall range of 800 - 2000 mm and growth has been correlated with rainfall (Pan *et al.*, 1980; Cai *et al.*, 1984; Yang *et al.*, 1981). That *C. lanceolata* can survive in low rainfall areas (*ca.* 800 mm) is due to the summer rainfall pattern; the species has however been described as susceptible to drought (see chapter XV).

Plant moisture stress (PMS) can be directly measured from the plant itself. However water stress depends upon a number of factors; in the first instance water availability (which depends upon amount of water in the soil and soil type), and also temperature and humidity. There are also a number of methods for inducing water stress in plants such as using solutions of varying solute concentrations as the growing medium; periodic watering to field capacity followed by drying to a specified PMS (drying-wetting cycles); and maintaining the soil (growing media) at specified soil moisture levels. This last method can be accurately measured by soil water potential which is a measure of how tightly water is held in the soil; or less accurately by calculating the water holding capacity

of the soil (field capacity) and varying amounts of water added to the soil in relation to this.

The aim of this experiment was to examine growth of *C. lanceolata* seedlings in response to three different water stress treatments, as well as the seedlings' ability to recover from imposed long term water stress. Growth was measured by biomass as well as long and short term physiological responses. Water stress was imposed by holding soils at various levels relative to field capacity. This method is cheaper and easier to set up than measuring soil water potential, and simulates long term water stress conditions which is not achieved by drying-wetting cycles.

2. MATERIALS AND METHODS

One-year-old seedlings were used in this experiment. Seedlings were previously grown in nursery beds, and in winter were lifted and potted into PB $1^1/_2$ bags with commercial potting mix (and 3 month fertiliser). The seedlings were previously used in the mid-winter frost resistance experiment where they were exposed to frosts of -8, -12 or -15 ^oC. Seedlings were then placed under shade cloth for the remainder of the 1989 winter.

In late September 1989 seedlings of healthy appearance were selected from seedlings which had received either -8 or -12 ^oC frosts. These seedlings were then re-potted into PB $6^1/_2$ bags with sieved (< 4 mm) commercial potting mix, and fresh weights were recorded. Seedlings were watered to field capacity to allow for transplanting shock and then dried to one of three water stress levels.

Once the desired level was reached the PB bags were enclosed in plastic bags loosely secured around the stem to prevent evaporation from the soil surface. Watering was applied through two plastic tubes inserted into the soil at depths of 5 and 10 cm.

2.1 Provenance Material

Seven provenances (PV) were represented: PV's 1 - 5, 9, and 10. Provenance details are given in appendix A.

Two replicates (blocks) based on seedling fresh weights at the time of re-potting were used. Within each block, three seedlings from each provenance were represented in each stress level, however seedling mortality reduced final numbers to two (or occasionally one) seedlings. Seedling mortality occurred *early* on in the experiment which may have indicated some transplanting shock; mortality was mostly in the greatest stress level (Low, 30% of FC) which suggested that water stress either directly caused mortality or accentuated transplant shock.

2.2 Treatment Conditions

Three water stress levels were chosen, based upon earlier calculations of field capacity (FC) of the potting mix: High, 100% of FC; Medium, 60% of FC; Low, 30% of FC.

Seedlings were weighed every two or three days and water was added, to the required weight. In late December sample plant moisture stress measurements showed very little difference between high and medium water levels, it was therefore decided to reduce the medium level to 15%. Treatments were subsequently relabelled as:

SL 1	100% FC	(formerly High, 100% FC)
SL 2	30% FC	(formerly Low, 30% FC)
SL 3	15% FC	(formerly Medium, 60% FC)

Some tip dieback occurred initially at SL 3 (see Plate 9.1) but the plants as a whole tended to recover and produce new growth. Water stress levels were imposed on the seedlings from mid-October through to mid-March.

Seedlings were grown over summer in a glasshouse set at 25 ^{o}C and temperatures were on average close to this, although temperature extremes ranged from 10 ^{o}C at night to 40 ^{o}C during mid-day.

2.3 Measurements

Percentages of seedling mortality (SM) were recorded prior to the reorganisation of stress levels. Following mortality, seedlings were reordered to obtain a more balanced design; unstressed seedlings were allowed to dry down to stressed levels where mortality had reduced seedling numbers.

Stem diameters were recorded at the beginning and end of the experiment and the difference was expressed as a percentage of growth (D%).

Diurnal photosynthesis rates and stomatal resistances (PS_{stress} and SR_{stress} respectively) were measured on sample seedlings from block 1 in late-February using the LI-6200 portable photosynthesis system (LI-COR, Lincoln, Nebraska, USA). One seedling per provenance x stress level combination was used. Plant moisture stress (PMS) for all seedlings was then measured using a pressure chamber (PMS Instruments inc., Corvallis, Oregon, USA). Two readings per plant were taken; pre-dawn PMS (PD_{stress}) and mid-day PMS (MD_{stress}); the difference between these two readings ($M\text{-}P_{stress}$) was also calculated. Pressure chamber technique, preparation of material and precautions in taking of measurements are discussed in Kramer (1983), Ritchie and Hinckley (1975), and Turner (1981).

Block 2 was then harvested together with most of block 1. The sample seedlings (used in PS_{stress} and SR_{stress}) from block 1 were then re-watered to field capacity for two weeks and then measured for PMS ($PD_{recovery}$, $MD_{recovery}$ and $M\text{-}P_{recovery}$) and diurnal photosynthesis and stomatal resistance ($PS_{recovery}$ and $SR_{recovery}$). Sample seedlings were then harvested and leaf areas for PS measurements were taken with a Delta-T area meter.

Seedlings were individually harvested and separated into root (R), old stem (S_O), old leaves (L_O), current season's stem (S_n) and current season's leaves (L_n) components. These were oven dried at 70 ^oC for at least 48 hours and then weighed. Total weight (T), root : leaf+stem (R:LS), root : total (R:T), stem : total (S:T), leaf : total (L:T), current season's growth : total (LS_n:T) ratios and current season's growth as a percentage of old growth (LS%) were derived from the dry weights.

2.4 Analysis

Analysis of variance (ANOVA) was performed on all variables. The General Linear Model (GLM) procedure was used to account for the unbalanced number of seedlings in each class. The ANOVA format was as follows:

Source	Degrees of Freedom		
Block	1	1	-
Stress Level (SL)	2	2	2
Provenance (PV)	6	6	6
SL x PV	12	12	-
Error	20	46	12
TOTAL	41[i]	67[ii]	20[iii]

[i] for SM

[ii] for D%, PD_{stress}, MD_{stress}, $M\text{-}P_{stress}$, and T, R, S_O, L_O, S_n, L_n, R:LS, R:T, S:T, L:T, LS_n:T, LS%.

[iii] for $PD_{recovery}$, $MD_{recovery}$, $M\text{-}P_{recovery}$ and both sets of PS and RS.

Diurnal PS and SR measurements were also graphically compared, as time of measurements, temperature and light conditions were not consistent.

3. RESULTS

3.1 Seedling Mortality

There were highly significant differences observed between water levels (high, medium, and low); seedlings subject to low water levels had the greatest mortality while those under high water levels had the least. There were no significant provenance differences. Results are given in Table 9.1, significance in Table 9.2.

While the results indicate that *C. lanceolata* suffers high mortality at low water levels it must be remembered that this may have been induced or compounded by transplant shock. Subsequent results below are from the reordered seedlings where there was no further mortality even after drying down to lower water levels, which suggests that well established seedlings are able to tolerate low water levels. There was considerable tip dieback on seedlings at SL3 but the species' ability to resume growth from adventitious buds below the injury site did not result in further large scale mortality (see Plate 9.1).

3.2 Dry Weights and Derived Values

Significant provenance differences were observed in L_O, S_O and LS%. Differences in old foliage and stems are to be expected as seedling size originally varied between provenances; these measurements are therefore not included in further analysis or discussion. LS% was greatest in PV5 with over 320 % growth of new (above ground) tissue; other provenances ranged from 160 to 239 % but were not significantly different at $p = 0.05$.

Differences between stress levels were significant for L_n, LS:R and LS%. In all cases SL1 had the greatest values, followed by SL3 and then SL2. Typical growth responses are shown in Plate 9.2. LS% also showed a significant SL x PV interaction. Mean values of these variables are shown in Table 9.1. Pr > F values for all variables are given in Table 9.2.

3.3 Plant Moisture Stress

Plants showed highly significant differences between stress levels for PD_{stress}, MD_{stress}, and $M\text{-}P_{stress}$. SL3 in all cases had the most negative PMS, followed by SL2 and SL1. There was also a difference between provenances in PD_{stress}, with PV2 and PV4 ($PD_{stress} > 6.0$ bars) being significantly greater then PV10 ($PD_{stress} = 3.7$ bars).

In contrast PMS (recovery) measurements of sample seedlings re-watered to FC were not different in any of the recovery variables and were very close to SL1 in the stressed measurements.

Pr > F values are given in Table 9.2 and mean values are given in Table 9.3.

3.4 Stem Diameter Growth

Increase in stem diameter was significant between stress levels but not provenances. As before SL1 had the greatest growth (22.1 %), while SL2 and SL3 had half as much (11.2 and 10.6 % respectively). Values are given in Tables 9.1 and 9.3.

3.5 Photosynthesis and Stomatal Resistance

Polynomial curves were fitted to approximate diurnal patterns in all graphs (Figures 9.2 - 9.5), these are provided as a visual comparison only. Graphs of diurnal photosynthesis show differences in PS_{stress} between stress levels (Figure 9.2); SL1 seedlings generally appear to have higher PS_{stress} rates than those of SL2 and SL3. $PS_{recovery}$ differences (Figure 9.3) also follow this pattern. A similar trend is seen for SR_{stress} (Figure 9.4) and $SR_{recovery}$ (Figure 9.5) measurements (with SL1 having least stomatal resistance). However $SR_{recovery}$ differences are smaller compared to SR_{stress} differences, indicating that there was partial recovery.

ANOVA was carried out on the measurements to get an overall indication of PS and SR performance between stress levels. Although each individual measurement differed in terms of time, temperature and light conditions it was assumed that a comparison over the entire day would cope reasonably with these fluctuations. Results support the graphical interpretation although $PS_{recovery}$ and $SR_{recovery}$ for SL2 and SL3 did differ from those of SL1 but were closer to SL1 than those in the corresponding stressed measurements.

Table 9.2 gives the Pr > F values, mean values of PS and SR are given in Table 9.4.

4. DISCUSSION

Effects of water stress on plant species are well documented (*e.g.* Hsiao, 1973; Kramer, 1983; Kramer and Kozlowski, 1979). In general increased water stress results in decreased plant growth caused by decreased cell enlargement and reduced photosynthesis due to stomatal closure and reduced leaf area (Kramer, 1983). Drought conditioning in nursery studies also supports this. Seedlings grown at low temperatures and high drought stress were more drought resistant (compared to treatments with less drought stress and/or higher temperatures), but were smallest in size (Van den Driessche, 1991). Cell division is also affected which in turn affects growth; however this appears to be secondary to effects on cell enlargement (Boyer, 1976). The ability of a species to survive a given water stress therefore depends on its responsiveness to these factors.

4.1 Provenance Variation

This has been reported within a number of tree species *e.g. Pinus taeda, P. pinaster, Pseudotsuga menziesii, Eucalyptus spp.* (Bongarten and Teskey, 1986; Teskey *et al.*, 1987 Nguyen and Lambert, 1989; Kramer and Kozlowski,1979). Not surprisingly, resistance to injury, drought tolerance, or survival appears to be related to geographical origin: Trees from xeric environments are more likely to survive severe long term water stresses then those from mesic environments, but are usually not as productive overall (Teskey *et al.*, 1987).

In this experiment there were no significant differences other than LS% and PD_{stress}. It is somewhat surprising that LS:R did not show any differences as water stress seems to influence this ratio markedly. Teskey *et al.* (1987) reported that some provenances of *P. taeda* from xeric environments have greater relative root growth rates and lower relative leaf growth rates than others. A similar response was observed for *P. pinaster* (Nguyen and Lambert, 1989).

That some response was not evident may be due to the duration of the experiment (which ran for approximately 5 months). Over this period root growth in the PB bags resulted in almost all seedlings' root systems filling the bags and in some cases becoming root bound. Therefore root growth would have become restricted and any differences early on would have been negated.

LS%: While dry weight differences were not significant, new above ground growth as a percentage of old above ground growth (LS%), did show a significant difference between PV5 and other provenances. This implies that LS:R's may have differed given either a shorter duration or larger soil volume. PV5 is the most interior of the provenances (appendix B) and has less rainfall than other southern provenances (appendix A), it is therefore surprising that LS% was greatest for PV5, as the reverse would have been expected.

From Table 9.1 there appears to be an inverse relationship between initial biomass (L_O + S_O) and LS%. PV5 was the smallest provenance and exhibited the most new growth (on a percent basis). It is common to find smaller seedlings having greater relative growth rates than larger seedlings, and this is probably the case in this experiment. Again root growth maybe a confounding influence as PV5 seedlings were the smallest throughout the experiment. Thus their root systems did not occupy as much space in the PB bags, perhaps enabling greater shoot growth due to relatively greater amounts of nutrients and water being available (or less limiting).

PMS: These measurements similarly showed some provenance difference in PD_{stress}. Pre-dawn measurements are considered to be the most useful PMS reading as they reflect

when conditions in the soil-plant-atmosphere system are in equilibrium throughout (Myers, 1988; Walters and Reich, 1989).

PV2 and PV4 (southern provenances) had significantly greater pre-dawn stress levels than PV10 (a northern provenance). While this was not the case for other PMS measurements the overall trend for PD_{stress} showed southern provenances to have greater stress readings (PV's 1-5) then the northern ones (PV's 9, 10). A similar trend was apparent in LS%.

In a study in Taiwan there was racial (family) variation in drought resistance, generally those from higher latitudes and altitudes were more resistant and drought resistant families were also resistant to $KClO_3$ toxicity (Hwang, 1974). Overall however, there appears to be little difference between provenances. This is consistent with earlier findings for *C. lanceolata* in other provenance-physiological experiments.

4.2 Stress Levels

Differences between levels were more significant and meaningful than provenance differences. Many of the dry weight variables were not significant and again this is most likely due to the root growth. Another factor which must also be considered is that SL3 was maintained at a higher soil water content for the first half of the experiment so that long term growth differences would have been reduced. However this was not the case for more immediate measures of PMS, PS and SR.

New leaf growth, $\mathbf{L_n}$, at SL1 was almost 50% heavier than SL3 or SL2 and this would have caused the observed difference in **LS:R** values as R and S values were similar for all levels. As mentioned above LS:R is highly influenced by stress levels. Root/shoot ratios of two *Eucalyptus* species increased with increased stress (Bachelard, 1986). This pattern is generally followed although the converse is implied by Squire *et al.* (1987) for *Pinus radiata* where root growth was more reduced then shoot growth. *C. lanceolata* is consistent with the norm and the differences may have even be more accentuated if root growth was unrestricted by the PB bags.

D% was also consistent, with SL1 having almost twice as much increase as the other levels. Again there would have been some confounding of SL3 effects due to changing water levels but in some seedlings at this level stem diameter actually decreased suggesting that this may not be as sensitive as the dry weight measures. Carbon allocation to the roots increases at high stress levels at the expense of the stem (Teskey *et al.*, 1987). Change in allocational patterns such as root/shoot ratios in response to stress have been reported by Reich *et al.* (1989). It is possible that stem diameter shrinkage occurred as a result of translocation; certainly the stem component was lower in SL3 then

SL1. Stem shrinkage in response to water stress has been well documented in other species (Kramer and Kozlowski, 1979).

LS% was also significantly greater in SL1. The other levels were again similar in response. This clearly demonstrates that *C. lanceolata* prefers very large amounts of water for optimum (above ground) growth and is sensitive to decreases in water availability. The extent of new shoot growth at the various stress levels is seen in Plate 9.2.

PMS_{stress} measurements verified the findings for the above dry weight variables. PMS measurements are more accurate than dry weights (in this experiment) in the sense that they are an immediate measure of the plant's water status (rather than a long term morphological measure). A short term physiological response such as this is not always a good indicator of long term performance (Myers, 1988) but for this experiment, PMS is not dependant on the changing of stress levels for SL3. This was shown by the significant differences in PD_{stress} and MD_{stress} between SL2 and SL3.

Furthermore as plants were maintained at set stress levels it may be assumed that the differences observed in the PMS measurements would have resulted in distinct morphological differences if the confounding effects were removed.

$PMS_{recovery}$ measurements were very similar between "treatments" indicating that plant recovery was achieved in two weeks. All measurements were within one bar of the PMS_{stress} measurements for SL1 (field capacity).

PS and **$SR_{recovery}$** measurements indicated that only partial recovery was achieved as there were still differences between SL1 and the others. However the differences between SL1 and SL2 (while significant) were not as great as those for PS and SR_{stress}. This would suggest that cellular differences between stress levels had developed over the experiment. SR measurements appear to be higher than in other species. Maximum SR for *Alnus glutinosa* at severe stress was between 13 and 17 s cm^{-1} (Hennessey *et al.*, 1988), whereas *P. taeda* grown under a dry regime had an SR of about 8 s cm^{-1} (Bongarten and Teskey, 1986). SR of open stomata for various species are reported by Kramer and Kozlowski (1979) and range from 0.65 to 11.30 s cm^{-1}.

It is likely that stomatal closure especially during mid-day would have resulted in the high values in this experiment. The use of a gas flow to measure PS and SR can cause stomatal closure if the pressure is too high (Raschke, 1975) so this is also a possibility. Nevertheless the trend of increased resistance with increased stress is still consistent with other results and it may be that *C. lanceolata* has higher stomatal resistance compared to more temperate species reported here.

PS measurements are also low compared with those at similar stress levels in *Ulmus americana* (Walters and Reich, 1989) but are similar to other PS measurements of *C. lanceolata* grown under high temperature (28 ^{o}C) in an earlier experiment (chapter VI). Decreased PS rates between treatments is undoubtedly due to stomatal closure and thus restriction of CO_2 diffusion (Boyer, 1976). Decreased chloroplast activity may also cause decreased PS under low light conditions due to decreased electron transport (Boyer, 1976) but this is unlikely given the large growth response at all levels.

4.3 Comparisons With Field Studies

Field studies in Queensland, Australia have indicated that *C. lanceolata* is sensitive to drought conditions and that poor survival results (P. Nielsen, pers.comm.). *C. lanceolata* is also commercially grown in Brazil on a small scale. It is however confined to the central coastal areas where rainfall is abundant and there is little or no moisture deficit (IBDF, 1971; Golfari, 1968). It has been abandoned in areas with a pronounced moisture deficit (Golfari, 1968).

In China *C. lanceolata* is restricted to areas where mean annual rainfall (summer pattern) is between 800 and 2000 mm, with best growth occurring in areas where mean annual rainfall is above 1000 mm (China, Cooperation Group of Chinese fir, 1981). There is an absence of water deficit in these areas (Watts, 1969). Root development and tree growth was correlated with humus content and this is closely related to soil moisture status (Li *et al.*, 1981). Exposure of seedlings to direct sunlight before planting resulted in water losses of 10 - 40 %; seedling survival following planting was correspondingly reduced to 87 - 63 %, compared with 95 % in controls (Liu, 1963). The overall ecological picture indicates that this is a high moisture demanding species, sensitive to drought.

Cultural practices at the nursery stage have been shown to influence PMS levels in *C. lanceolata*. Growing media that did not retain water after irrigation resulted in lesser seedling growth (than media which retained water); PMS was also greater and sustained, with the result that seedlings were more drought resistant (Shen *et al.*, 1988). Similarly seedlings raised in dibbling tubes had lower potential for fast growth compared with those raised in nursery beds and plastic bags, but had developed drought tolerance (Fang *et al.*, 1988). Frequent irrigation of seedlings in media with high water retention capacity produced succulent seedlings with poor resistance to water stress (Shen, 1989). Seedlings then can be cultured to withstand drought but this appears to be at the expense of growth.

That growth still occurred at high water stresses (SL2 and SL3) indicates that either *C. lanceolata* is able to withstand low soil water conditions or that experimental conditions were not inducing enough stress. The latter is more probable: extensive root systems at all stress levels would have resulted in uptake of a large amount of the added water as

roots would be in close proximity to the water. Soil water content around the watering tubes would thus be close to field capacity. In addition, the media being potting mix holds a large amount of water compared to natural soils. Thus even at SL3 water was probably still readily available and in sufficient supply for growth. A useful measure is soil moisture stress (potential) which indicates how tightly the water is held in the soil; this was unable to be measured in the experiment.

However, given that growth in the unstressed seedlings (SL1) was on average 1.4 - 1.5 times greater (LS%) and twice as much (D%) as that of stressed seedlings it is clear that *C. lanceolata* has a marked preference for ample water supply.

5. SUMMARY

Significant mortality occurred between initial water stress levels, with most mortality occurring at the lowest level. However subsequently, well-watered seedlings were able to be dried down to lower water levels without any further mortality, indicating that well established seedlings can develop some tolerance to low water levels. Growth of *C. lanceolata* seedlings was affected by water stress, with significant increases of growth in unstressed seedlings compared with stressed seedlings. Container restrictions meant that usual characteristics of water stress on seedling growth were not evident, at least in the long term morphological sense.

More immediate physiological measures further demonstrated the difference between stressed and unstressed seedlings, although seedling survival was unaffected. These short term measures would have resulted in more distinct differences in morphological characteristics, given the absence of container restrictions. Recovery of seedlings after stress was imposed for $4^1/_2$ months was apparent, but not complete within two weeks of rewatering stressed seedlings to field capacity. Short term PMS measurements of sample seedlings were similar to unstressed seedlings, but PS and SR measurements were not, indicating that morphological change at the cellular level may have occurred.

There was very little provenance difference in terms of any measure. Growth was significant for one provenance but this may have been an artefact of the experimental conditions. That little variation was observed is not too surprising given that the provenances have exhibited little or no differences in other physiological and growth experiments.

Table 9.1a: Mean Values of Dry Weights and Derived Measurements by Provenance

	PV1	PV2	PV3	PV4	PV5	PV9	PV10
L_o (g)	5.572 ^{a}	4.924 ^{ab}	3.701 ^{b}	4.190 ^{ab}	1.829 ^{c}	4.256 ^{ab}	3.613 ^{b}
S_o (g)	6.065 ^{a}	4.284 ^{b}	3.379 ^{bc}	3.523 ^{bc}	1.991 ^{c}	3.561 ^{bc}	3.788 ^{bc}
Ln (g)	13.496 ^{ab}	14.285 ^{a}	11.428 ^{ab}	12.802 ^{ab}	8.538 ^{b}	12.263 ^{ab}	12.172 ^{ab}
S_n (g)	3.678 ^{a}	2.251 ^{ab}	1.692 ^{ab}	1.654 ^{ab}	1.306 ^{b}	2.116 ^{ab}	2.384 ^{ab}
R (g)	13.670 ^{a}	10.803 ^{ab}	11.255 ^{ab}	9.891 ^{ab}	6.949 ^{b}	9.812 ^{ab}	12.650 ^{a}
T (g)	37.403 ^{a}	34.961 ^{ab}	31.455 ^{ab}	32.060 ^{ab}	20.613 ^{b}	32.007 ^{ab}	34.608 ^{ab}
LS:R	2.593	2.367	1.860	2.407	2.466	2.642	1.919
LS:T	1.015	0.690	0.645	0.685	0.674	0.701	0.634
R:T	1.421	0.310	0.355	0.315	0.326	0.299	0.366
S:T	1.465	0.186	0.163	0.158	0.158	0.182	0.183
L:T	0.6517 ^{a}	0.4997 ^{ab}	0.4822 ^{ab}	0.5273 ^{ab}	0.5164 ^{ab}	0.5185 ^{ab}	0.4509 ^{b}
LS_n:T	0.813	0.419	0.416	0.436	0.489	0.463	0.416
LS%	160.27 ^{b}	168.05 ^{b}	189.83 ^{b}	191.56 ^{b}	320.53 ^{a}	239.40 ^{b}	193.78 ^{b}
D%	13.761	13.759	12.847	14.305	19.052	13.708	19.020
SM (%)	44.4	38.8	33.3	20.0	23.5	33.3	38.8

n.b. Values with the same or no letter are not significantly different at the 95% level. See section 2.3 for definitions of variables.

Table 9.1b: Mean Values of Dry Weights and Derived Measurements by Stress Level

Variable	SL1 (100% FC)	SL2 (30% FC)	SL3 (15% FC)
L_o (g)	3.935	4.093	4.225
S_o (g)	4.048	3.682	3.773
L_n (g)	15.296 [a]	10.041 [b]	11.188 [b]
S_n (g)	2.985	1.887	1.544
R (g)	11.243	10.998	9.939
T (g)	36.868	28.585	30.670
LS:R	2.890 [a]	1.797 [b]	2.306 [ab]
LS:T	0.711	0.772	0.679
R:T	0.289	0.227	0.321
S:T	0.198	0.687	0.170
L:T	0.513	0.544	0.509
LS_n:T	0.498	0.555	0.422
LS%	260.56 [a]	170.65 [b]	192.68 [b]
D%	22.074 [a]	11.246 [b]	10.608 [b]
SM (%)	(High) 11.9 [a]	(Med) 32.1 [b]	(Low) 55.9 [c]

n.b. Values with the same or no letter are not significantly different at the 95% level. See section 2.3 for definitions of variables.

Table 9.2: Probability (Pr > F) Values

Variable	PV	SL	PV x SL
L_o (g)	*0.0048*	0.9910	0.3989
S_o (g)	*0.0013*	0.5546	0.7732
Ln (g)	0.3340	*0.0009*	0.9655
S_n (g)	0.2240	0.0728	0.4327
R (g)	0.1771	0.6993	0.7859
T (g)	0.3436	0.0562	0.9490
LS:R	0.5066	*0.0058*	0.6906
LS:T	0.1935	0.5893	0.2827
R:T	0.3592	0.2616	0.3389
S:T	0.3019	0.3533	0.3239
L:T	0.1764	0.6868	0.2715
LS_n:T	0.3776	0.5950	0.2854
LS%	*0.0125*	*0.0137*	*0.0195*
D%	0.8873	*0.0017*	0.6478
SM	0.3804	*0.0001*	0.2562
PD_{stress}	*0.0498*	*0.0041*	0.0598
MD_{stress}	0.7168	*0.0001*	0.8740
$M\text{-}P_{stress}$	0.3999	*0.0001*	0.4476
$PD_{recovery}$	0.6894	0.8326	--
$MD_{recovery}$	0.3519	0.4884	--
$M\text{-}P_{recovery}$	0.6648	0.6971	--
PS_{stress}	--	*0.0001*	--
SR_{stress}	--	*0.0001*	--
$PS_{recovery}$	--	*0.0001*	--
$SR_{recovery}$	--	*0.0337*	--

Table 9.3a: Mean Values of Plant Moisture Stress (bars) by Provenance

	PV1	PV2	PV3	PV4	PV5	PV9	PV10
PD_{stress}	-5.045 ab	-6.187 a	-4.864 ab	-6.150 a	-4.357 ab	-4.625 ab	-3.667 b
MD_{stress}	-9.773	-9.375	-9.182	-11.950	-10.321	-9.396	-9.306
$M\text{-}P_{stress}$	-4.727	-3.188	-4.318	-5.800	-5.964	-4.771	-5.639
$PD_{recovery}$	-3.333	-3.000	-2.833	-3.167	-3.000	-3.333	-3.500
$MD_{recovery}$	-5.333	-5.500	-5.667	-7.000	-5.167	-7.000	-6.333
$M\text{-}P_{recovery}$	-2.000	-2.500	-2.833	-3.833	-2.167	-3.667	-2.833

Table 9.3b: Mean Values of Plant Moisture Stress (bars) by Stress Level

	SL1 (100% FC)	SL2 (30% FC)	SL3 (15% FC)
PD_{stress}	-4.167 b	-4.729 b	-6.275 a
MD_{stress}	-6.948 c	-10.094 b	-13.137 a
$M\text{-}P_{stress}$	-2.781 b	-5.365 a	-6.862 a
$PD_{recovery}$	-3.214	-3.071	-3.214
$MD_{recovery}$	-6.429	-5.643	-5.929
$M\text{-}P_{recovery}$	-3.214	-2.571	-2.714

n.b. Values with the same or no letter are not significantly different at the 95% level. See section 2.3 for definitions of variables.

Table 9.4: Mean Values of Photosynthesis and Stomatal Resistance by Stress Level

Variable	SL1 (100% FC)	SL2 (30% FC)	SL3 (15% FC)
PS_{stress} [1]	2.407 [a]	1.628 [b]	1.462 [b]
SR_{stress} [2]	14.271 [a]	24.092 [b]	29.804 [b]
$PS_{recovery}$	2.451 [a]	1.772 [b]	1.716 [b]
$SR_{recovery}$	13.646 [a]	16.904 [ab]	17.830 [b]

n.b. Values with the same or no letter are not significantly different at the 95% level.

[1] PS units are μmol m^{-2} s^{-1}. SR units are s cm^{-1}.

Figure 9.1: Plant Moisture Stress Measurements

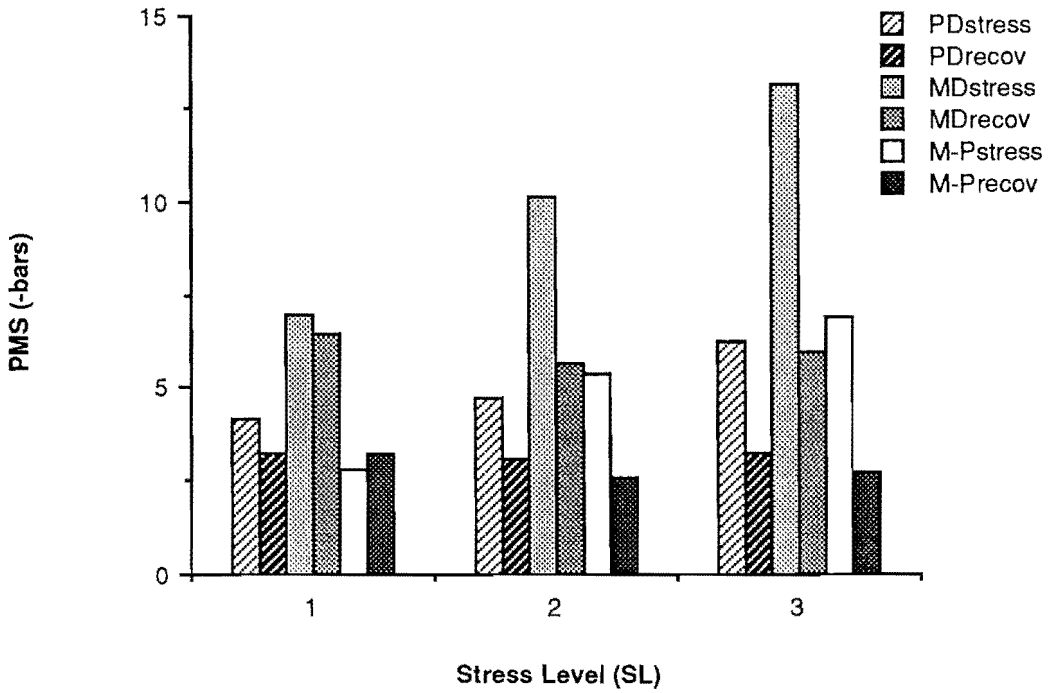


Figure 9.2: Photosynthesis (of Stressed Seedlings) by Stress Level

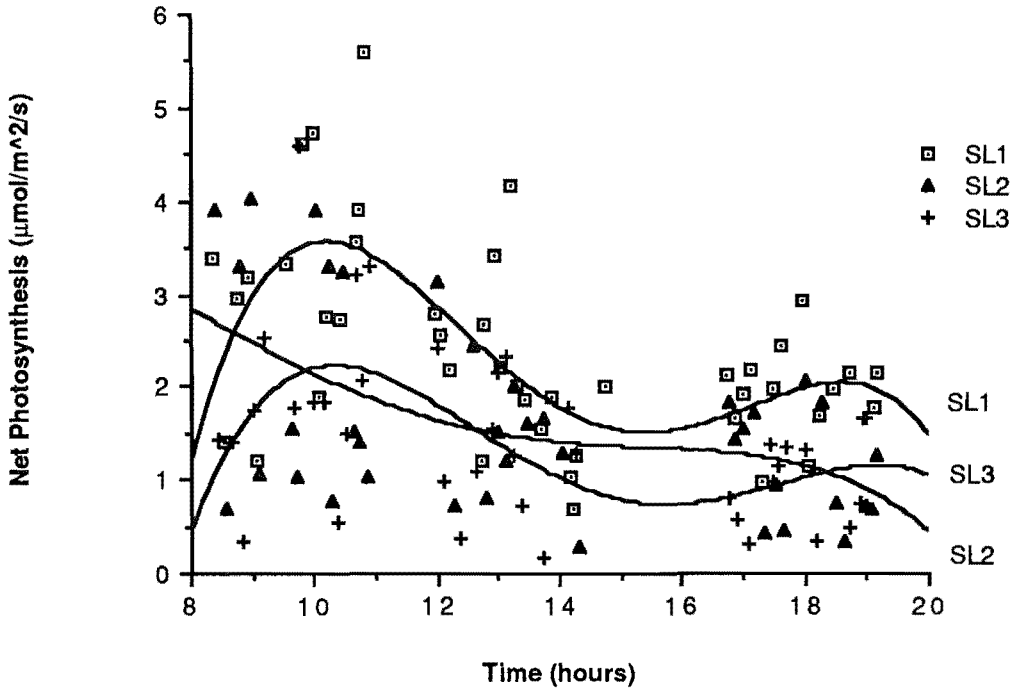


Figure 9.3 Photosynthesis (Following Recovery) by Stress Levels

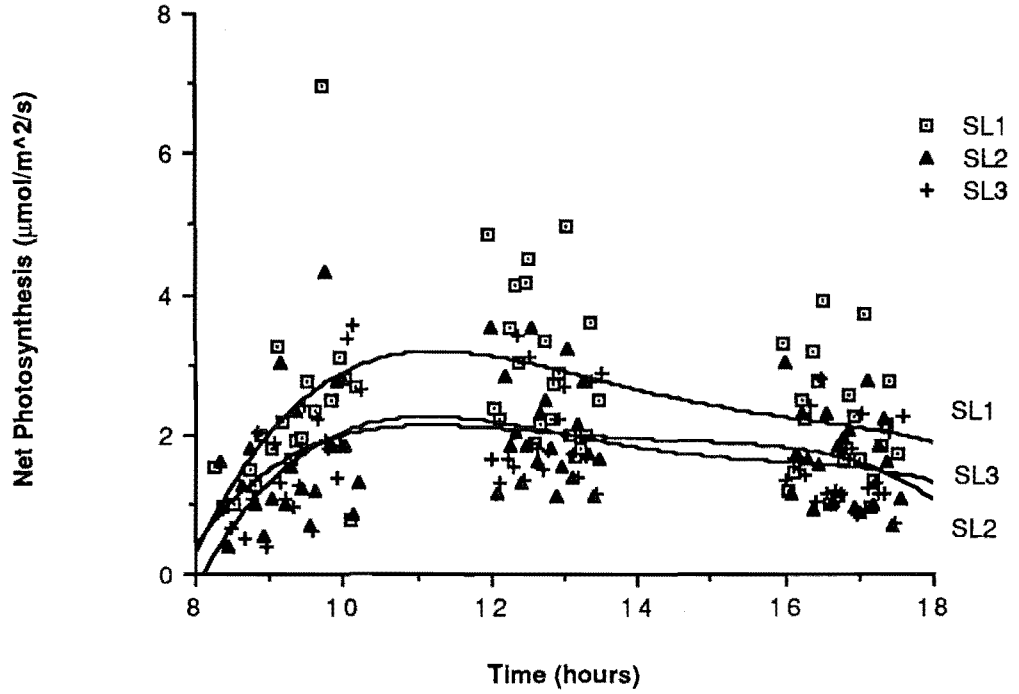


Figure 9.4: Stomatal Resistance (of Stressed Seedlings) by Stress Level

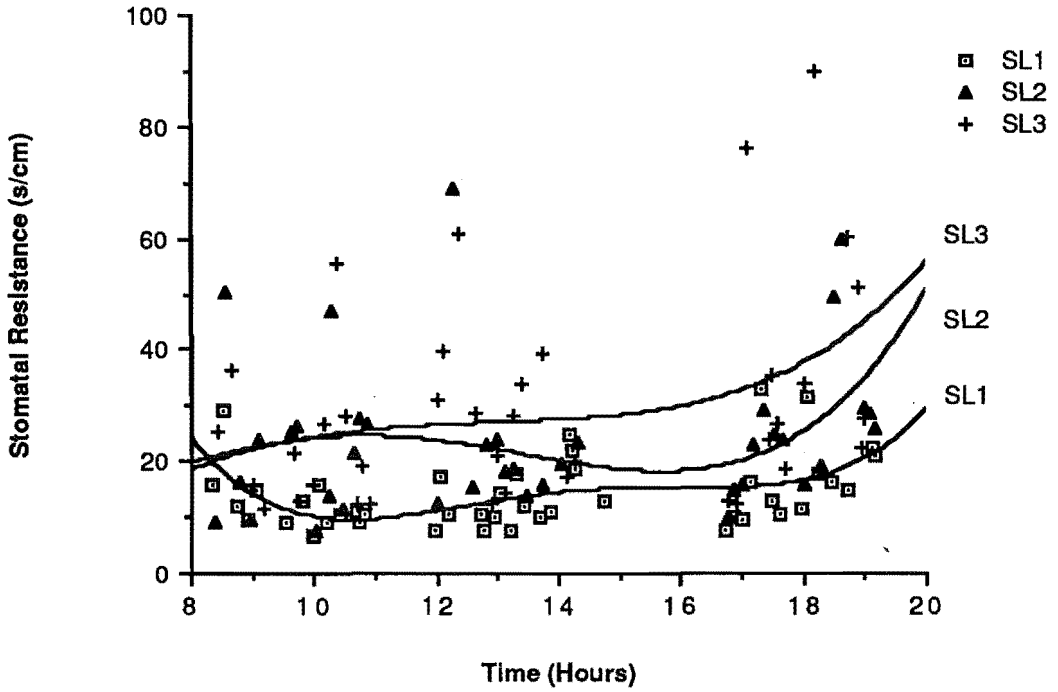


Figure 9.5: Stomatal Resistance (Following Recovery) by Stress Level

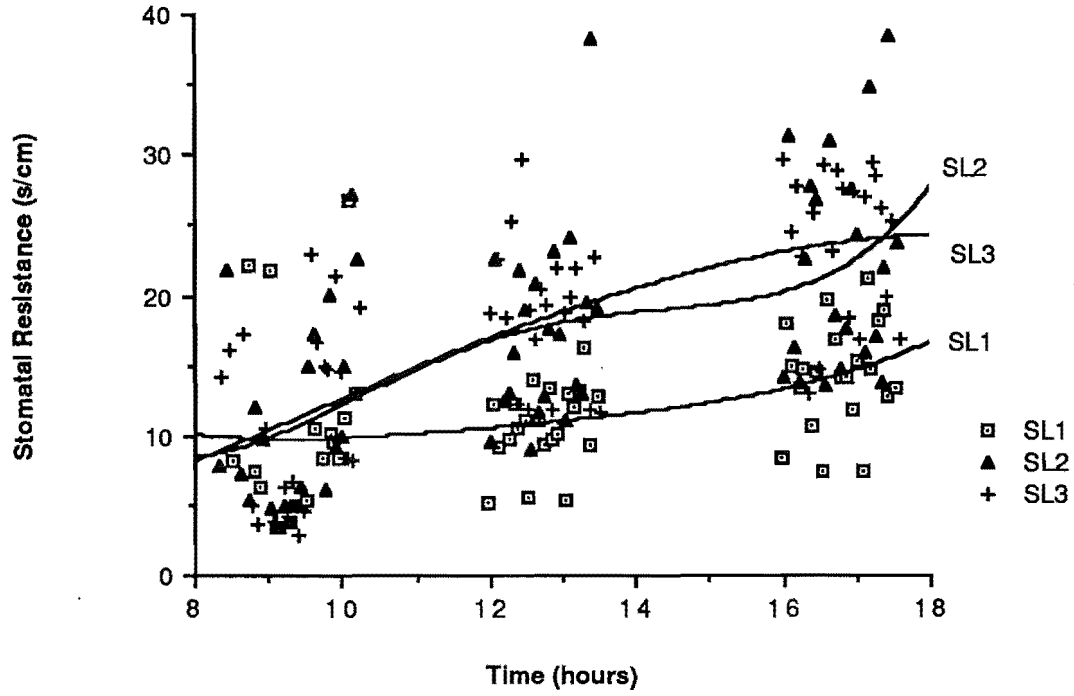


Plate 9.1: Detail of Tip Dieback at SL3

(note new growth from adventitious buds at the leading shoot and the far lateral shoot)

Plate 9.2: Seedling Growth Response to Water Stress

(From left to right: SL1; SL2; SL3. New leading shoot growth is from the 1st set of branches on each seedling)

CHAPTER X

GROWTH RESPONSE OF SEEDLINGS TO NUTRIENT LEVELS AND MYCORRHIZA COLONIZATION

1. INTRODUCTION

Mineral nutrition is essential for successful growth and plays an important role in physiology. Nutrients are used in plant tissue, catalysts, osmotic regulators, buffer systems, and regulation of membrane permeability (Kramer and Kozlowski, 1979). Nitrogen (N) in particular is vital for plant growth; nitrogen deficiency is the second most common limitation to growth, after water stress. Nitrogen is used in proteins (in protoplasm of new cells and as enzymes) and chlorophyll, and the demand for nitrogen is closely related to growth (Kramer and Kozlowski, 1979). Nitrogen nutrition controls vegetative growth rate of a plant due to its role in protein metabolism (Mengel and Kirby, 1979).

Nitrogen is commonly the fourth most abundant element in plants after carbon oxygen and hydrogen (Epstein, 1972). After nitrogen a number of elements are considered essential for plant survival if: i) Plants cannot complete their life cycle without it, and ii) it is part of an essential plant constituent (Epstein, 1972). A vast number of nutrient trials using solutions of varying mineral element compositions have been carried out for plant species, Hoagland's solution and subsequent modifications have been popular choices for tree species, as has Ingestad's solution.

C. lanceolata is part of the Taxodiaceae family which forms vesicular-arbuscular mycorrhizal (VAM) associations (Molina and Trappe, 1984). VAM, unlike ectomycorrhizas show little or no host specificity (Molina and Trappe, 1984; Fitter and Hay, 1984), which may explain the world-wide distribution of VAM species and wide range of host plants (Gerdemann, 1975; Nicholson, 1975). Hu (1981) reported association of *C. lanceolata* with *Glomus fasiculatus* at high altitudes on poor sites. There is also an association with *Gigaspora gigantea* which is most abundant in winter and least in spring-summer (Hu, 1986). *C. lanceolata* does not form ectomycorrhizal associations; in a trial with other conifer species, seedlings were grown with spore and vegetative innoculum of *Pisolithus tinctorius*, but no associations were found (Hua *et al.*, 1991).

VAM colonization is considered beneficial to the host plant as VAM improve nutrient uptake generally (Molina and Trappe, 1984) and especially that of phosphorous (Fitter and Hay, 1981). Other benefits include drought resistance, ability to withstand high temperatures, and protection against pathogens (Molina and Trappe, 1984; Powell and Bagyaraj, 1984; Jackson and Mason, 1984).

The aim of this experiment was to quantify growth response of *C. lanceolata* seedlings to various levels of nutrients as well as VAM colonization. Nutrient levels were designed to range from deficiency to excess, while VAM colonization was attempted over all seedlings.

2. MATERIALS AND METHODS

Seed from the twelve provenances were soaked for 24 hours then stratified at 4 ^{o}C for four weeks. After stratification seeds were sown in trays containing commercial seed raising mix, and germinated. Forty three days after sowing, seedlings were transplanted into 120, 160 mm x 120 mm plastic pots containing sterile vermiculite and mycorrhiza-colonized roots of *Dacrycarpus dacrydioides* (collected from Deans Bush, Christchurch) and *Sequoia sempervirens* (from FRI, Rotorua).

2.1 Provenance Material

The provenances analysed in the experiment were: PV's 2 - 5, 7 - 11. Provenance material was pooled according to growth zones (China, Cooperation Group of Chinese fir, 1981b) and similar latitudes. Five groups were used in this experiment. Provenances were grouped as follows:

Group 1 - PV's 2 and 3 (zone II_{3c}).
Group 2 - PV's 4 and 7 (zone II_{3b}).
Group 3 - PV 5 (zone II_2).
Group 4 - PV's 8 and 9 (zones I_1, I_2) + PV 11 as filler.
Group 5 - PV 10 (zone I_2).

See appendices A and B for locations and details of provenances. Several provenances were not included, due to lack of germination (PV 6, zone II_{3b}) or adequate representation of their zone (PV's 1, 11 and 12, zone II_{3c}).

2.2 Treatment Conditions

After transplanting, seedlings were placed under glass. Each pot consisted of four seedlings from one of the groups and received one of six nutrient levels. The experiment was arranged in four blocks, blocked by initial size.

Nutrient solutions were applied weekly to each pot; all six were based on a modified half-strength Hoagland's Solution as used by the Plant Physiology Division, DSIR, Palmerston North (see appendix E). The compositions are given in Table 10.1 and were labelled as NL1, 5, 10, 100, 200, 600; reflecting the relative concentrations of macroelements.

The solutions were applied from the top of the pots and allowed to drain into dishes. Every two weeks the dishes were rinsed and cleaned with distilled water and the water re-applied to the pots. The vermiculite was kept moist by regular top watering with distilled water. Pots were randomised within blocks, and re-randomised every three weeks.

The experiment was carried out in a glasshouse with a limited amount of control over temperature. A Campbell Data Logger 21x measured hourly temperature, light and relative humidity for the duration of the experiment. Conditions are as given below:

	mean	(day)	(night)
Temperature (^{o}C):	23	26	18
Relative Humidity (%):	74	63	86
Light (μmol m^{-2} s^{-1}):	370		

The experiment ran for 85 days over summer (November 1988 to February 1989).

2.3 Measurements

At the conclusion of the experiment, measurements of stem diameter at ground level (D) were taken.

Seedlings were then individually harvested and roots were stained for vesicular-arbuscular mycorrhiza (VAM) using the KOH and lactophenol trypan blue method as given by Philips and Hayman (1970). The roots were then visually assessed for VAM colonization using the Institute for Mycorrhizal Research and Development, USDA Forest Service, Athens, Georgia (Kormanik and McGraw, 1982) classification system, modified as follows:

Class:	1	2	3	4
% Colonization:	0 - 5	6 - 25	26 - 50	50+

Root material was then oven dried for 72 hours at 70 ^{o}C and then weighed (R). Above ground material was separated into stem and leaf components, oven dried for stem, leaf and total above ground dry weights (S, L, LS respectively). Total plant weight (T) was calculated from R and LS and derived ratios of leaf to shoot (L:S), leaf to root (L:R), leaf to total (L:T), shoot to root (S:R), and shoot to total (S:T) were also calculated.

Finally nutrient analysis of the dried plant tissue was carried out at the Forestry Research Centre, Ilam. Above ground plant tissue (stem and leaf) was bulked according to nutrient level x VAM class and analysed for N, P, K, Ca and Mg contents. Because of financial constraints, only three nutrient levels (10, 100, 200) were analysed.

2.4 Analysis

Analysis of variance (ANOVA) of seedlings was carried out for the variables D, L, S, R, T and the derived ratios L:S, L:R, L:T, S:R, S:T. The experiment was analysed in two separate analyses; firstly by provenance groups (GP), and secondly by VAM classes (VC).

As analysis was done by either GP or VC; the General Linear Model (GLM) procedure was used to account for the unbalanced number of seedlings in each class. The ANOVA format for a two factorial randomised block design was as follows:

Source	Degrees of Freedom	
Block	3	3
Nutrient Level (NL)	5	5
VC	3	-
GP	-	4
NL x VC	14	-
NL x GP	-	20
Error	60	87
TOTAL	85	119

Tissue analysis of N, P, K, Ca and Mg was carried out for three nutrient levels (NL 10, 100, 200). Seedlings were bulked in each block by NL and VC and statistically analysed using the GLM procedure. The ANOVA format was as follows:

Source	Degrees of Freedom	
	design	actual
Block	3	3
NL	2	2
VC	3	3
NL x VC	6	6
Error	33	27
TOTAL	47	41

3. RESULTS

Analysis by both GP and VC gave significant differences, however analysis by VC also showed significant interaction with nutrient level (NL). Block effects were also significant indicating that blocking by initial size was justified.

3.1 Analysis by Provenance Groupings

Highly significant differences were found between NL ($p = 0.0001$) for all measured variables, significant and highly significant differences were also found between GP for all biomass measures and for L:S. There was no interaction between NL and GP. Probability ($Pr > F$) values are given in Table 10.2.

Nutrient level: Weight and diameter differences were not significant at the lower levels (NL 1 - 10), but were so at the higher levels. NL 200 gave the greatest weight response followed by NL 600 and 100. Weights, other than R, at NL 200 were significantly greater (at the 95% level) than those at NL 100, while NL 600 gave weights intermediate between these two. The greatest proportional increase in weights and diameter was between NL 10 and 100. Increased diameter growth corresponded to increase in NL with significant differences between each of the higher levels (NL 100, 200, 600).

A similar pattern was found with the derived ratios. Differences between the lower and the higher levels were not as significant (especially for L:S) although in general NL 600 and NL 200 had the largest values. Table 10.3 shows all variables with significance values.

Differences in appearance between NL were also observed. In general seedlings at NL 1 -10 showed severe browning (terra cotta, Munsell ref. 10R 4/8) of the older leaves while new growth had a pale, sea green colouration (7.5GY 6/6) indicating a chlorotic condition. Leaves were thin and small. This is similar to symptoms of nitrogen deficiency described in Kao *et al.* (1973). Seedlings in NL 100 had a deeper grass green leaf colouration (7.5GY 4.5/8) although there were exceptions (Plate 10.1). Browning of old leaf tips was still present although not as frequent; leaves were thicker and larger.

Seedlings in NL 200 and 600 were similar in size to those in NL 100 but leaf colouration was somewhat paler and occasionally yellow-green. As before some slight browning of the tips was seen in some seedlings.

Root systems also differed between high and low treatments. Seedlings in NL 1 - 10 had thin succulent roots, mostly unbranching. Those of the higher treatments were more

branched and fibrous; the lower portions were thick and succulent, while older portions were suberised.

Provenance Groups: A general trend was seen in all biomass measures except R with GP5 having the greatest biomass, followed by GP's 3, 2, 1, and 4 respectively. In all cases GP's 5 and 3 were significantly greater than GP4. The trend was reversed for the derived ratio L:S, GP4 had the largest value while GP5 had the smallest. Mean values are given in Table 10.4.

Provenance differences in response to nutrients are generally considered unimportant. This is not because differences do not exist (*e.g. Pinus sylvestris, P. taeda,* Goddard and Hollis, 1984; *Larix laricina*, Wanyancha and Morgenstern, 1987), but rather that within provenance variation is usually greater than between provenance variation and appears to be an adaptation strategy allowing growth on a wide range of sites (Goddard and Hollis, 1984; Wanyancha and Morgenstern, 1987). The analysis that follows is therefore based on VAM classes as opposed to grouping as the differences in groups may have merely been due to differing initial seedling sizes.

3.2 Analysis by VAM Classes: Measurements

Highly significant differences between NL were observed in all measured variables D, L, S, T and L:T. Differences between VC were also apparent in D, L, S and T. NL x VC interaction was seen in L, S and T. Probability (Pr > F) values are given in Table 10.2.

Nutrient level: Subsequent re-analysis by VC did not significantly alter rankings and differences between nutrient levels. There were changes in values but these were very small. The observations given in the above section (3.1) apply to the re-analysed results. Table 10.5 shows all variables with significance values. Using T as an example, the effect of NL on biomass production is illustrated in Figure 10.2.

Mycorrhizal classes: All biomass measures, and D increased with increasing colonization. Growth response to different classes was seen between the heaviest (VC4, 50% or more) and lightest (class 1, 0-5%) colonization levels. In all the above cases with the exception of S, VC4 gave significantly heavier dry weight than the other levels. Intermediate levels (VC2 and 3) were not significantly different from each other (Table 10.6). The clear trend in increased biomass with increasing colonization suggests that there is a positive correlation of growth with mycorrhizal colonization.

NL x VC interaction: While overall differences in VC were apparent, a more significant response was seen in the interaction between NL and VC for all weights and L:T. Further analysis was carried out for VC by NL to see if differences were apparent within NL (Table 10.7).

VC had no significant effect at lower NL (1 - 10), but a clear response was seen in NL 100 with VC4 giving greater weights. This trend was not apparent in NL 600, here VC3 (26-50%) gave the best response while VC4 was not significantly different from VC1. Results are graphically shown for T in Figure 10.1. More interestingly, weight response at heavier VC appeared to be similar at higher NL (VC4 in NL 100, 200 and VC3 in NL 200, 600). Weights in light VC in NL 100 were similar to those of the lower NL solutions.

L:T differences between VC's were significant at NL 200 with heavy VC showing greater allocation of biomass to leaves compared to light VC. This trend was not seen at NL 600 where VC4 had the lowest L:T, similar to VC1 but significantly lower than those of VC2 and 3.

3.2 Analysis by VAM Classes: Tissue Analysis

There were significant responses to NL by N P K and Ca, but not for Mg; however as Mg did not vary between NL, this was not unexpected. The response to VC was not significant except in K and Mg. Probability (Pr > F) values are given in Table 10.8.

Nutrient level: Increased uptake of N, P, K and Ca was associated with increasing NL. For N and P, differences in uptake were significant between all NL solutions; for Ca, uptake was significantly greater in NL 200; and for K, uptake was significantly less in NL 10 (Table 10.9).

Mycorrhizal classes: While response was not as significant as NL there was a significant difference between VC's for uptake of K; with increased uptake associated with increased colonization. Uptake of Ca and Mg showed a negative trend with increased colonization. Values are given in Tables 10.10 and 10.11.

4. DISCUSSION

In this experiment it appears that seedling growth responded primarily towards increased nutrient levels. Although there were significant differences between groups no clear trend was apparent. Both GP4 (smallest seedlings) and GP5 (largest seedlings) were from similar latitudes and therefore had similar climates; the intermediate GP's were from lower latitudes. As mentioned above, provenance variation is usually not an important factor in nutrient uptake. It is more likely that these differences may have been a result of initial seedling size.

Mycorrhizal colonization also affected growth, although only within NL 100 and 200. Results show that greatest growth occurred at high nutrient levels (NL 100 - 600) *and*

high mycorrhizal colonization levels. Growth was least at low nutrient levels (NL 1 - 10); mycorrhizal classes did not give significantly different responses at these levels.

4.1 Nutrient Levels

Best overall weight growth within nutrient levels occurred in NL 200 (Figure 10.2) which had a high concentration of macro elements (*e.g.* 210 ppm N). This contrasts with an earlier study of *C. lanceolata* seedlings by Chen and Walker (1982) in which greatest weight response (over 168 days) was seen in nutrient levels very similar to those of NL 100 used here (*i.e.* ppm's of: 105 N, 15.5 P, 97.8 K, 100.2 Ca, 24.3 Mg, 32 S). It should be noted that Chen and Walker did not go beyond these levels and thus their findings do not necessarily contradict the results obtained here.

However, studies of other coniferous species generally give optimum nutrient levels below those of NL 200. Fowells and Kraus (1959) found that *Pinus taeda* and *P. virginiana* seedlings had greatest weight growth at 100 ppm N (out of 1, 5, 25, 100, 200 and 400 ppm N), with seedlings showing deficiencies at 1 and 5 ppm N. Conversely both species grew well at all levels of P tested (400 - 0.1 ppm), with 1 ppm P showing the greatest growth. This was attributed to mycorrhizal formations which were absent at higher levels of P. Similar results were obtained by Pharis and Kramer (1964) for N nutrition of *P. taeda* .

Will (1961) found the optimum nutrient levels for *Pinus radiata* seedlings grown in both water and perlite cultures to be 105 ppm for N, 0.93 ppm P, 117 ppm K, and 23 - 253 ppm Mg. As before satisfactory growth was obtained at low P levels.

Van den Driessche (1968) compared relative growth rates (RGR) of *Pseudotsuga menziesii* and *Picea sitchensis* ; both species showed best RGR at 50 ppm N, 30 ppm P and 20 ppm K. Similar "low" levels were also found by Ingestad (1959) working with *Picea abies*. Best growth was obtained with a solution of 50 N, 10 P, 50 K, 40 Ca, and 15 Mg (all ppm). Reed *et al.* (1983) examined the effects of light and nitrogen on growth of *Pseudotsuga menziesii* seedlings and found best growth regardless of light intensity to be between 39 - 77 ppm N.

Examples of species with "high" nutrient requirements include *Larix laricina* where growth increased with increased N to 200 ppm (Wanyancha and Morgenstern, 1987a), and *Pinus strobus* at (in ppm) 300 N, 350 P, 150 K, 200 Ca (Mitchell, 1939 as reported by Chen and Walker, 1982). *Pinus banksiana* seedlings also appear to have a high optimum N level of 200 - 250 ppm (Bensend, 1943 as reported by Pharis and Kramer, 1964).

It would appear that optimal or normal nutrient levels for conifer seedlings vary between species, but generally occur at lower levels than those found in this experiment. While

experiment conditions such as nutrient composition and supply, duration and timing, seedling age *etc.* do not permit direct comparisons with other studies, this experiment showed that *C. lanceolata* appears to prefer relatively high nutrient levels for growth. Curve fitted data ($r^2 = 0.5476$) of total dry weights shows this preference (Figure 10.3) and indicates that the optimal range is between 300 and 400 ppm N (in between NL 200 and 600).

Zhang *et al.* (1980) found that *C. lanceolata* plantations in mountainous areas were more productive than hill and hilly lowland areas. A number of factors are undoubtedly involved in determining overall productivity (*e.g.* drainage, precipitation, relative humidity *etc.*), but it is interesting to note that these (mountainous) areas had generally higher levels of fertility (*i.e.* greater organic matter, N, P and available K). Field nutrient requirements of *C. lanceolata* are considered larger than broadleaved trees; uptake is greater and returns through litterfall are smaller (Li, 1981). Nutrient cycling is more dependent upon rainfall than litterfall for N, K and Mg; while Ca and P are returned primarily through litterfall. Leached nutrients comprise some 48 - 53% of returned nutrients (Ma, 1988).

The high uptake and low return of nutrients serves to lower soil fertility. After three rotations, growth of *C. lanceolata* was 24.3% less than that of the first rotation; and total soil organic matter and total and available N, P, K had decreased by 18 - 45% (Fang, 1987). Fertiliser application is therefore necessary to maintain site productivity. In a pot trial, nitrogen fertilisation of seedlings has shown that growth, chlorophyll content, photosynthesis and respiration increased with increasing urea application up to an optimum (Fan and Yu, 1987). The optimum range of urea was 0.8 - 1.2 g per pot (range tested was 0 - 2.0 g per pot). Response to K has also been measured; application of K promoted uptake of N, P and K, as well as improving resistance to diseases and low temperature and photosynthesis (Li, 1988). Biomass (dry weight) increased by 8.7 - 26.5%. Field trials of Ca, Mg, and P greatly accelerated growth of 3 year old trees; shoot growth by as much as 80 % and dbh by 29 - 34 % (Li *et al.*, 1987).

The seemingly large nutrient requirement for optimum growth in the experiment in this thesis may be an artefact. Due to practical considerations, top application of the nutrient solutions was carried out weekly, with distilled water applied every two to three days. Thus it may be that while initial concentrations of nutrients were high, actual supply over the duration of the week could well have been low. However as nutrient solutions were applied at the same time and with the same volumes, the results are still comparable and demonstrate the effects of relative nutrient levels rather than actual supply/concentration *per se*.

That the frequency of application may have been important in determining exact optimum levels could also have been borne out by general seedling appearance. As mentioned

above, browning of older leaves / leaf tips was present throughout all treatments although severity and frequency decreased from NL 100 upwards. This could have been due to lack of supply of some elements which may have been rectified had more frequent watering of solutions occurred.

Similarly, while NL 200 showed the greatest growth response, seedlings in both NL 200 and 600 were paler (almost chlorotic) in leaf colouration compared to those in NL 100. This could have been due to toxicity effects or nutrient imbalances at these higher levels; again more frequent solution watering may have made the effect more noticeable in terms of growth. Frequency of application of solutions at above optimum concentrations has been shown to reduce drought resistance (Pharis and Kramer, 1964). It was suggested that this may have been a result of nitrogen imbalance causing metabolic problems.

Nutrient availability may have also been influenced by pH as this affects solubility and ionic form of some elements (Epstein, 1972). Nutrient solutions had a pH range of 4.5 (NL 600) to 6.2 (NL 1), and thus it is possible that many elements may have been less available at the upper extreme (NL 600), or that Mn and B may have been limited at NL 1 (Mengel and Kirby, 1979). However it is accepted that most plant species grow well between pH 5 - 7 (Epstein, 1972) and that good growth occurs over a wide range of pH if essential minerals are present (Kramer and Kozlowski, 1979). *C. lanceolata* is reported as growing in pH 4 - 9.4 (Cai *et al.*, 1984) and best growth between pH 4.5 - 6.5 (FAO, 1982), therefore it is unlikely that pH would have had a significant effect on growth in this experiment.

Root systems were long, thin and unbranched at lower nutrient solutions, and thicker and fibrous at higher nutrient solutions (see Plate 10.2). The trend of long, thin roots at deficient levels of N and P is well known (*e.g.* Ingestad, 1959; Fowells and Kraus, 1959; Will, 1961). This, as well as the general depression of growth and seedling appearance, indicates that NL 1 - 10 were below normal nutrient levels necessary for good growth.

Tissue analysis of above ground biomass (leaf and stem components) for seedlings in NL 10, 100 and 200 confirmed the trend of increased growth with increased nutrient level: All nutrients showed greater uptake with increased nutrient level (Table 10.9 and Figure 10.4).

Of more interest is the actual percentages (by dry weight) obtained. In comparison with other studies the amount of N, P, K, Ca and Mg in the leaves/stems appeared to be within the range for optimal growth. Ingestad (1959), for example, found that *Picea abies* has optimal contents which are exceeded in this experiment in NL 100 and 200. This is also the case with for *Pinus radiata* (Will, 1961), and *Pseudotsuga menziesii* (Youngberg, 1984; van den Driessche, 1984). P contents for *Pinus taeda* and *P. virginiana* are also

below those reported here (Fowells and Kraus, 1959), as are those for *Larix laricina* (Wanyancha and Morgenstern, 1987b).

Chen and Walker's (1982) findings for N content are also below those of NL 100 and 200, however P content is reasonably close. Similar results for N content are seen in *Pinus taeda* (Pharis and Kramer, 1964; Fowells and Kraus, 1959) and *P. virginiana* (Fowells and Kraus, 1959). These findings are summarised in Table 10.12, marginal levels are given in brackets. For *C. lanceolata* K, Ca and Mg contents appeared to be generally high for seedlings in all three solutions. N and P contents were also high for NL 100 and 200, however nutrient deficiencies in this experiment were most likely from NL 10 downwards with respect to N and (possibly) P.

4.2 Mycorrhizal Colonization

Results show that VC gave significant responses in **weight and diameter growth.** While the magnitude of the response to VC was not as large as that of NL, the results indicate that mycorrhizas are of some importance in growth. There was visual evidence of the benefits of VAM colonization in a pretrial test in potting mix (Plate 10.3). VAM colonized seedlings were healthier and larger in appearance and seedling mortality was slight compared with non-colonized seedlings, however no biomass measurements were made in this case.

VAM colonization in this experiment was only partially successful, failure by some seedlings to form VAM associations may have been due to inadequate or insufficient innoculum material. In general, conditions for colonization were acceptable; mean temperature was close to the optimal temperature range of 28 ^{o}C - 34 ^{o}C for colonization (Daniels Hetrick, 1984), and daylength was close to maximum. It is possible that low colonization may have been a result of low levels of appropriate VAM fungi. However VAM associations tend to be less host specific then ectomycorrhizae; in Taiwan, for example, 32 species of endomycorrhizae have been found in association with *C. lanceolata* and *Taiwania cryptomerioides* (Hu, 1988). Furthermore VAM species tend to have an extensive world-wide distribution.

Maximum colonization is expected to occur where fertility is low, and generally is associated with low P levels; however the extent to which soil fertility affects colonization can be mediated by the host plant's internal P content of the roots (Daniels Hetrick, 1984). The results from this experiment did not indicate that there was any relationship between colonization levels and nutrient levels. It is somewhat surprising then that there was no significant effect of VC at the lower nutrient levels where colonization would be expected to be greatest. Possibly the root systems of the seedlings at these levels were insufficiently branched to give large areas of contact with the root innoculum, while those

at the higher levels had larger root system and consequently more areas of contact and colonization.

As can be seen from Figure 10.1 there are considerable differences in weights of seedlings within VC at higher NL. Growth in VC4 at NL 100 is comparable to that at NL 200 (VC2 -4) and 600 (VC3). VAM colonization does not appear to be significant at NL 200 although there is a clear difference between no colonization (VC1) and colonization. The picture is further confused when considering why there should be significant responses either side of this nutrient level. Because mycorrhizal colonization was visually assessed the grading is subject to an inherently large margin of error. When assessment was made on the basis of colonization (VC2 - 4) or no colonization (VC1) then significant responses were seen in NL 100 - 600.

Tissue analysis showed slight differences of P content between non-mycorrhizal (VC1) and mycorrhizal (VC2 - 4) plants. Figure 10.5 illustrates the general trend of increased P uptake with increased colonization but the more significant effect is between nutrient levels. Certainly from Table 10.10 there is no significant effect of colonization on P uptake.

Comparing nutrient contents with weight increases does not appear to give a clear relationship. It would therefore seem to indicate that mycorrhiza does not affect N (Figure 10.6), P, Ca, and Mg uptake. This however is contrary to other findings and is probably due to the method of grading VC. Again if VC1 is compared to VC2 - 4 within each NL it is apparent that there is a difference in uptake. For K there is a significant effect of VC on uptake (Figure 10.7); the heavier the colonisation the greater the uptake. This however is not significant within NL again, demonstrating the large effect of NL on growth over VC.

5. SUMMARY

Nutrient requirements of *C. lanceolata* seedlings grown in vermiculite are relatively high. This experiment indicated that seedlings respond best to high levels of macroelements (210 ppm N, 31 P, 238 K, 200 Ca and 64 S), although possible toxicity/element competition effects may be starting to occur at this level. Good growth was also found at slightly lower levels (NL 100), but deficiencies became apparent below levels of 10.5 ppm N.

Nutrient contents of above ground tissue were also high (in comparison with other conifers) for seedlings grown in"high" levels of nutrients. Growth of seedlings in "low " nutrient levels was probably restricted by a deficiency of N.

Mycorrhizal colonization was not as significant as overall nutrient level in terms of growth. However this may have been due to the method of assessment adopted. Differences were apparent between mycorrhizal and non-mycorrhizal seedlings, with greater growth occurring in colonized seedlings at high nutrient levels.

Table 10.1: Nutrient Solution Composition (ppm)

Nutrient Level:	1	5	10	100	200	600
			Concentration (ppm)			
Nutrient						
N (NO_3)	1.05	5.25	10.51	105.06	210.12	630.36
P (PO_4)	0.16	0.77	1.55	15.49	30.98	92.94
K	1.19	5.95	11.90	118.95	237.90	713.70
S (SO_4)	0.32	1.60	3.21	32.08	64.16	192.48
Ca	1.00	5.01	10.02	100.20	200.40	601.20
Mg	----------2.08----------					
Fe	----------24.32----------					
B	----------0.250----------					
Mn	----------0.251----------					
Cu	----------0.010----------					
Zn	----------0.025----------					
Mo	----------0.005----------					
Cl	----------1.882----------					
Na	----------0.863----------					

Table 10.2: Probability (Pr > F) Values For Measured Variables

	D	L	S	LS	R	T
NL	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
GP	0.5934	0.0249	0.0001	0.0102	0.0006	0.0040
NL x GP	0.3304	0.6552	0.4373	0.6306	0.5266	0.6934
VC	0.0010	0.0020	0.0385	0.0026	0.0583	0.0023
NL x VC	0.1777	0.0006	0.0341	0.0010	0.0220	0.0008

	L:S	L:R	L:T	S:R	S:T
NL	0.0001	0.0001	0.0001	0.0001	0.0001
GP	0.0160	0.1296	0.1158	0.1295	0.2654
NL x GP	0.6446	0.7516	0.6234	0.8572	0.7913
VC	0.0644	0.9589	0.2129	0.1972	0.0676
NL x VC	0.1817	0.0673	0.0493	0.4328	0.4052

Table 10.3: Analysis by Provenance Groups: Mean Values For Variables At Given Nutrient Levels

NL:	D(mm)	L (mg)	S (mg)	LS (mg)	R (mg)	T (mg)
600	143.9 a	97.9 b	24.2 a	122.1 b	21.5 bc	143.6 b
200	133.6 b	120.6 a	26.8 a	147.3 a	23.7 a	171.0 a
100	121.0 c	94.9 b	19.8 b	114.7 b	28.7 b	143.4 b
10	89.3 d	50.0 c	9.8 c	59.8 c	18.6 cd	78.4 c
5	87.8 d	41.8 c	9.2 c	50.9 c	15.7 d	66.6 c
1	86.4 d	39.9 c	9.2 c	49.1 c	14.5 d	63.5 c

NL:	L:S	L:R	L:T	S:R	S:T
600	4.006 c	5.682 a	0.680 a	1.497 a	0.180 a
200	4.542 b	5.394 a	0.688 a	1.247 b	0.162 b
100	4.812 b	3.529 b	0.653 b	0.751 c	0.144 c
10	5.260 a	3.016 b	0.641 bc	0.595 c	0.128 d
5	4.622 b	2.966 b	0.629 c	0.666 c	0.141 c
1	4.444 b	3.065 b	0.629 c	0.722 c	0.147 c

values in the same column with the same letter are not significantly different at the 95% level.

Table 10.4: Analysis by Provenance Groups: Mean Values For Variables At Given Provenance Groups

GP:	L (mg)	S (mg)	LS (mg)	R (mg)	T (mg)	L:S
1	68.1 ab	15.4 bc	83.5 bc	22.1 a	105.7 ab	4.541 b
2	72.6 ab	16.3 b	88.9 abc	17.6 b	106.5 ab	4.601 ab
3	83.8 a	18.2 ab	102.0 ab	23.5 a	125.5 a	4.642 ab
4	62.6 b	12.7 c	75.0 c	15.6 b	90.6 b	4.966 a
5	83.9 a	19.9 a	103.8 a	23.3 a	127.1 a	4.323 b

values in the same column with the same letter are not significantly different at the 95% level.

Table 10.5: Analysis by VAM Classes: Mean Values For Variables At Given Nutrient Levels

NL:	D(mm)	L (mg)	S (mg)	LS (mg)	R (mg)	T (mg)
600	147.1 a	105.9 b	26.1 a	132.1 ab	23.0 b	155.1 ab
200	135.4 b	123.7 a	27.2 a	150.8 a	23.8 b	174.6 a
100	120.9 c	99.5 b	20.6 b	120.1 b	30.2 a	150.3 b
10	91.2 d	51.7 c	10.3 c	61.9 c	19.2 bc	81.1 c
5	88.5 d	42.3 c	9.1 c	51.4 c	16.4 cd	67.8 c
1	86.8 d	38.4 c	9.1 c	47.4 c	13.9 d	61.3 c

NL:	L:S	L:R	L:T	S:R	S:T
600	4.035 c	5.487 a	0.679 a	1.403 a	0.176 a
200	4.543 b	5.473 a	0.690 a	1.262 a	0.162 b
100	4.799 b	3.506 b	0.653 b	0.742 b	0.143 c
10	5.238 a	3.040 b	0.642 bc	0.605 b	0.129 d
5	4.666 b	2.845 b	0.625 c	0.638 b	0.139 cd
1	4.353 bc	3.021 b	0.627 c	0.721 b	0.150 c

values in the same column with the same letter are not significantly different at the 95% level.

Table 10.6: Analysis by VAM Classes: Mean Values For Variables At Given VAM Classes

VC:	D(mm)	L (mg)	S (mg)	LS (mg)	R (mg)	T (mg)
1	105.9 c	61.5 c	14.9 c	76.3 c	18.8 b	95.1 c
2	112.1 b	75.2 bc	16.7 bc	91.8 bc	20.1 b	111.9 bc
3	112.3 b	84.4 b	18.0 ab	102.4 b	21.4 b	123.8 b
4	127.7 a	98.7 a	20.5 a	119.2 a	28.2 a	174.4 a

values in the same column with the same letter are not significantly different at the 95% level.

Table 10.7: NL x VC Interaction. Mean Values of Significant Variables By NL

		Nutrient Level					
Var.	VC	1	5	10	100	200	600
L	1	43.6 a	39.5 a	45.6 a	61.7 b	93.9 a	84.7 b
	2	35.6 a	39.1 a	50.2 a	100.4 b	124.9 a	100.7 ab
	3	35.8 a	51.3 a	49.5 a	86.1 b	140.0 a	143.7 a
	4		36.5 a	61.6 a	149.9 a	147.9 a	83.4 b
S	1	10.2 a	8.5 a	9.0 a	15.4 b	24.5 a	21.6 a
	2	8.3 a	9.6 a	9.8 a	21.4 ab	26.0 a	24.9 a
	3	8.7 a	10.0 a	10.0 a	17.2 b	29.9 a	32.4 a
	4		7.7 a	12.2 a	28.5 a	29.5 a	25.3 a
LS	1	53.8 a	48.0 a	54.3 a	77.1 b	118.4 a	106.3 b
	2	43.9 a	48.6 a	60.1 a	121.8 b	150.9 a	125.5 ab
	3	44.5 a	61.3 a	59.5 a	103.2 b	169.9 a	176.0 a
	4		44.2 a	73.8 a	178.3 a	177.3 a	108.7 b b
R	1	16.3 a	14.4 a	17.1 a	22.9 b	20.1 a	22.1 a
	2	12.9 a	15.0 a	17.5 a	29.5 ab	26.5 a	19.4 a
	3	12.4 a	20.1 a	20.1 a	24.4 b	26.1 a	25.2 a
	4		16.1 a	22.1 a	44.1 a	21.4 a	27.7 a
T	1	70.0 a	62.4 a	71.3 a	100.0 b	138.5 a	128.4 b
	2	56.9 a	63.6 a	77.5 a	151.3 b	177.4 a	145.0 ab
	3	57.0 a	81.3 a	79.6 a	127.7 b	196.0 a	201.2 a
	4		60.3 a	95.8 a	222.4 a	198.7 a	136.5 ab
L:T	1	0.623 a	0.636 a	0.634 a	0.624 a	0.663 b	0.669 ab
	2	0.629 a	0.616 a	0.651 a	0.659 a	0.685 ab	0.689 a
	3	0.630 a	0.632 a	0.623 a	0.664 a	0.697 ab	0.709 a
	4		0.606 a	0.658 a	0.667 a	0.740 a	0.619 b

values in the same column with the same letter are not significantly different at the 95% level.

Table 10.8: Probability (Pr > F) Values For Elements

Element:	N	P	K	Ca	Mg
Source:					
NL	0.0001	0.0001	0.0001	0.0011	0.3497
VC	0.2459	0.0709	0.0020	0.2375	0.0109
NL x VC	0.0538	0.5613	0.0565	0.8326	0.7674

Table 10.9: Mean Values For Elements at Nutrient Levels

NL	N	P	K	Ca	Mg
200	2.640 ^{a}	0.359 ^{a}	1.521 ^{a}	0.375 ^{a}	0.436 ^{a}
100	2.250 ^{b}	0.304 ^{b}	1.511 ^{a}	0.308 ^{b}	0.413 ^{a}
10	0.995 ^{c}	0.172 ^{c}	1.034 ^{b}	0.309 ^{b}	0.437 ^{a}

values in the same column with the same letter are not significantly different at the 95% level.

Table 10.10: Mean Values For Elements At Mycorrhizal Classes

VC	N	P	K	Ca	Mg
4	1.979 ^{ab}	0.299 ^{a}	1.560 ^{a}	0.289 ^{b}	0.403 ^{b}
3	1.980 ^{ab}	0.288 ^{a}	1.409 ^{ab}	0.332 ^{a}	0.399 ^{b}
2	2.111 ^{a}	0.296 ^{a}	1.389 ^{b}	0.333 ^{a}	0.426 ^{b}
1	1.895 ^{b}	0.248 ^{a}	1.159 ^{c}	0.358 ^{a}	0.481 ^{a}

values in the same column with the same letter are not significantly different at the 95% level.

Table 10.11: Mean Values For Elements At Given NL and VC

NL	VC	%N	%P	%K	%Ca	%Mg
200	4	2.367 b	0.330 a	1.699 a	0.321 b	0.401 b
	3	2.572 ab	0.371 a	1.598 a	0.378 ab	0.397 b
	2	2.768 a	0.371 a	1.609 a	0.370 ab	0.421 b
	1	2.718 a	0.350 a	1.267 b	0.405 a	0.508 a
100	4	2.231 ab	0.332 a	1.733 a	0.282 b	0.404 ab
	3	2.371 a	0.322 a	1.628 a	0.302 ab	0.392 b
	2	2.290 ab	0.306 a	1.450 ab	0.297 ab	0.412 ab
	1	2.060 b	0.242 b	1.141 b	0.363 a	0.455 a
10	4	1.085 a	0.202 a	1.074 a	0.271 a	0.403 a
	3	0.998 a	0.182 bc	1.001 a	0.315 a	0.407 a
	2	0.994 a	0.172 ab	1.013 a	0.330 a	0.452 a
	1	0.947 a	0.153 c	1.064 a	0.307 a	0.473 a

values in the same column and same NL with the same letter are not significantly different at the 95% level.

Table 10.12: Optimum and Marginal (in brackets) Foliar Concentrations of Various Conifers

Species	N%	P%	K%	Ca%	Mg%
C. lanceolata [1]	1.81-2.03	0.14-0.29			
[2]	2.25-2.64 (0.995)	0.30-0.36	1.52	0.31-0.38	0.41-0.44
Picea abies [3]	2.0 (1.0)	0.2 (0.05-0.11)	0.9 (0.30)	0.08-0.19 (0.02)	0.11 (0.02-0.07)
Pinus radiata [4]	1.6	0.24	1.2	0.13	0.17
[5]	(1.2-1.5)	(0.11-0.14)	(0.3-0.5)	(0.10)	(0.10)
P. taeda [6]	1.7-2.3	0.14-0.18			
[7]	2.3-2.6				
P. virginiana [6]	3.1	0.14-0.18			
Pseudotsuga menzieseii [8]	1.8 (1.0-1.2)	0.18 (0.14-0.09)	0.8 (0.3)	0.20 (0.2)	0.12 (0.01)
Larix laricina [9]		0.10-0.14			

[1] Chen and Walker, 1982.
[2] Present study.
[3] Ingestad, 1959.
[4] Will, 1961.
[5] Mead, 1986.
[6] Fowells and Kraus, 1959.
[7] Pharis and Kramer, 1964.
[8] Youngberg, 1984; van den Driessche, 1984.
[9] Wanyancha and Morgenstern, 1987.

Figure 10.1: Mean Total Dry Weights by NL and VC

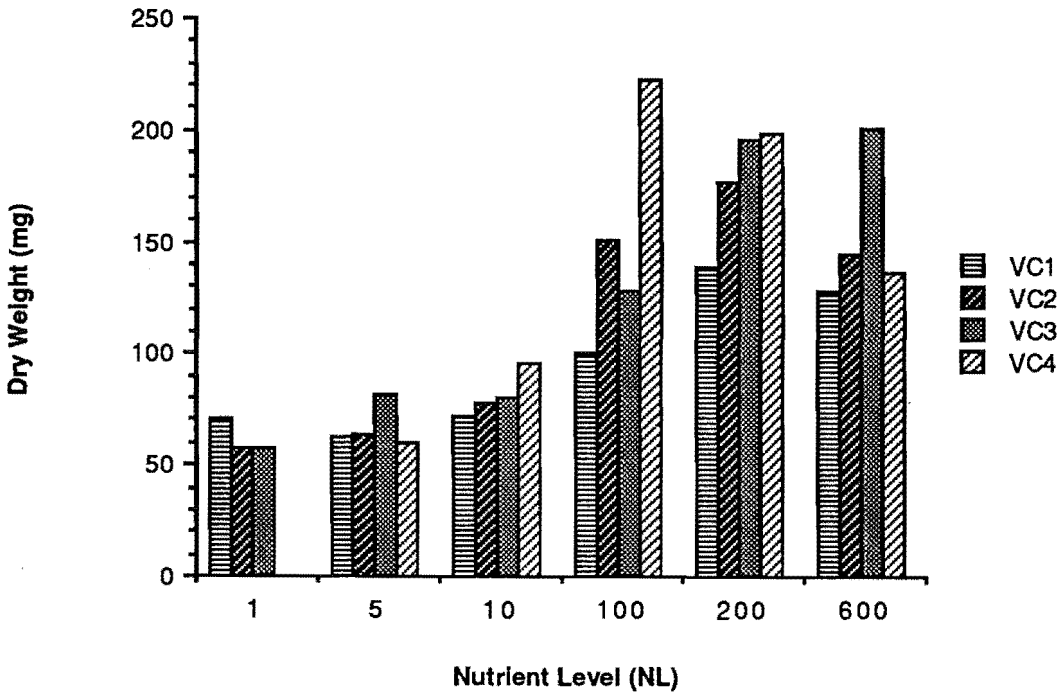


Figure 10.2: Mean Total Dry Weights by NL

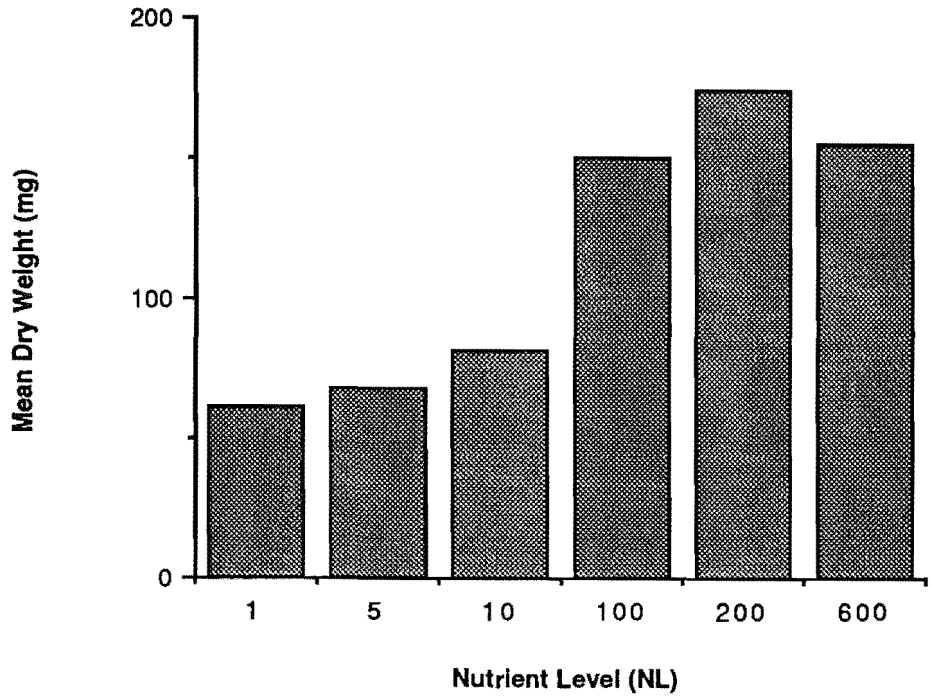


Figure 10.3: Total Dry Weights by NL

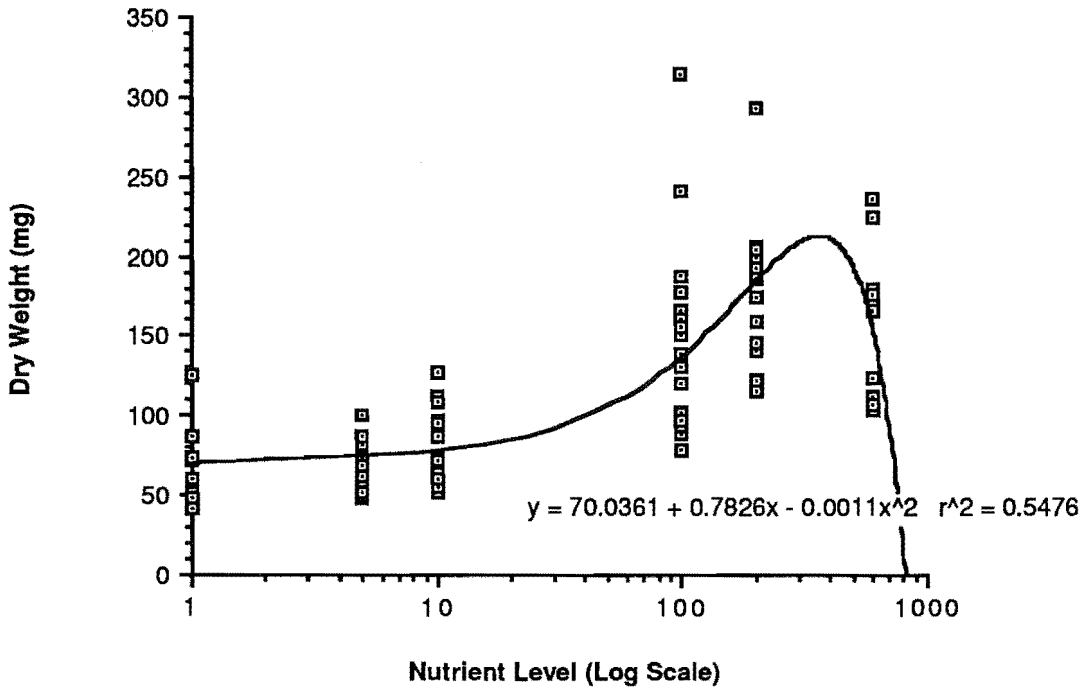


Figure 10.4: Plant Element Levels by NL

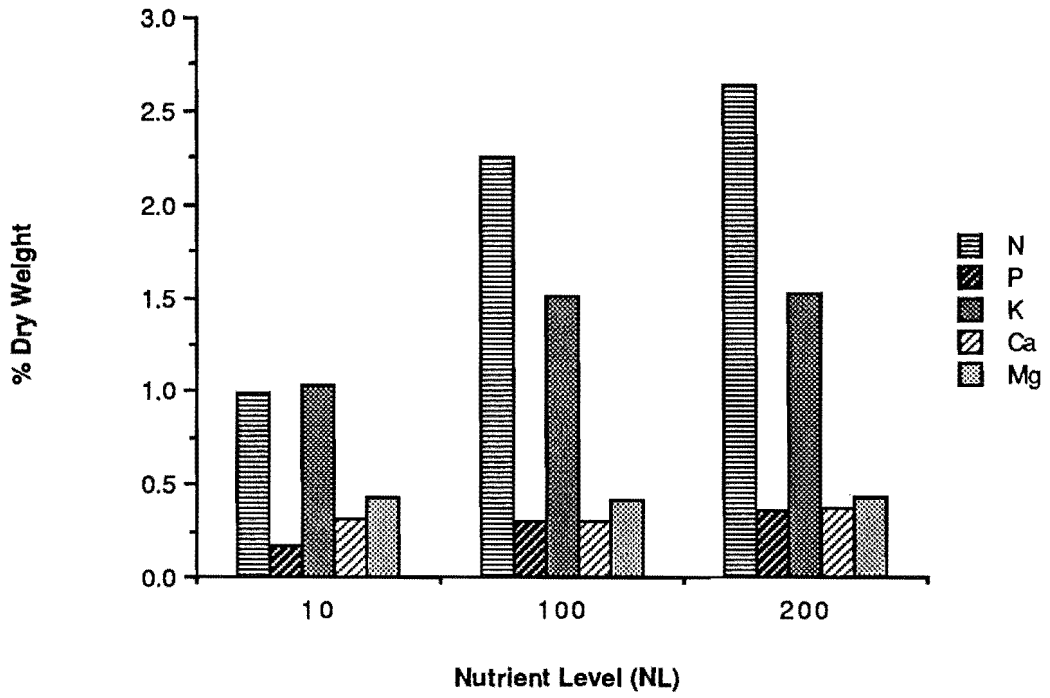


Figure 10.5: %P by NL and VC

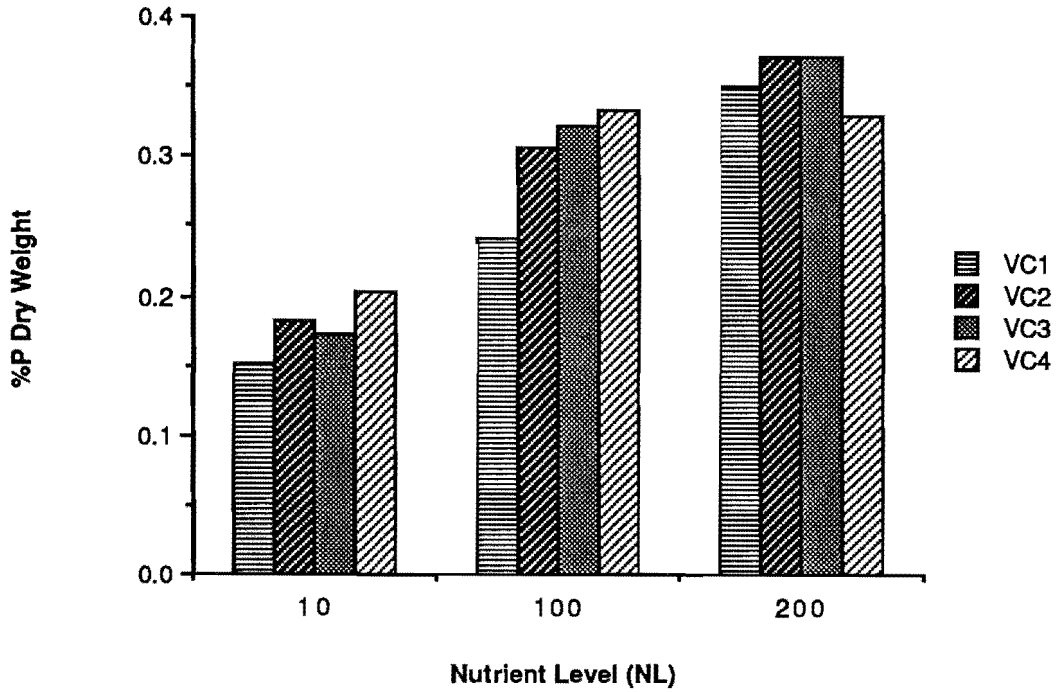


Figure 10.6: %N by NL and VC

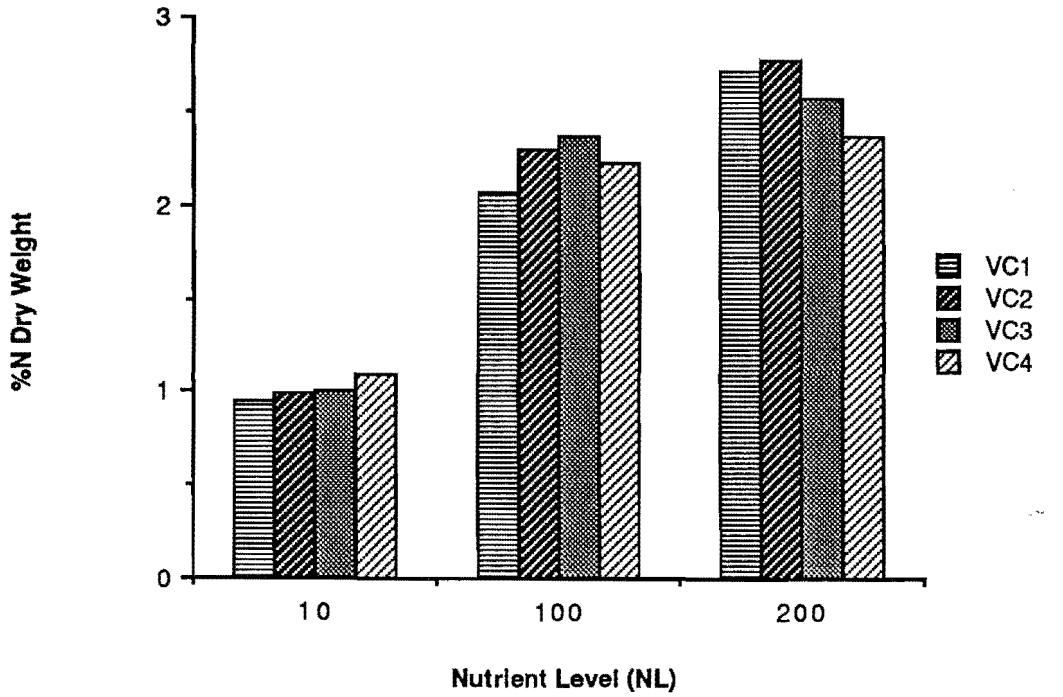


Figure 10.7: %K by NL and VC

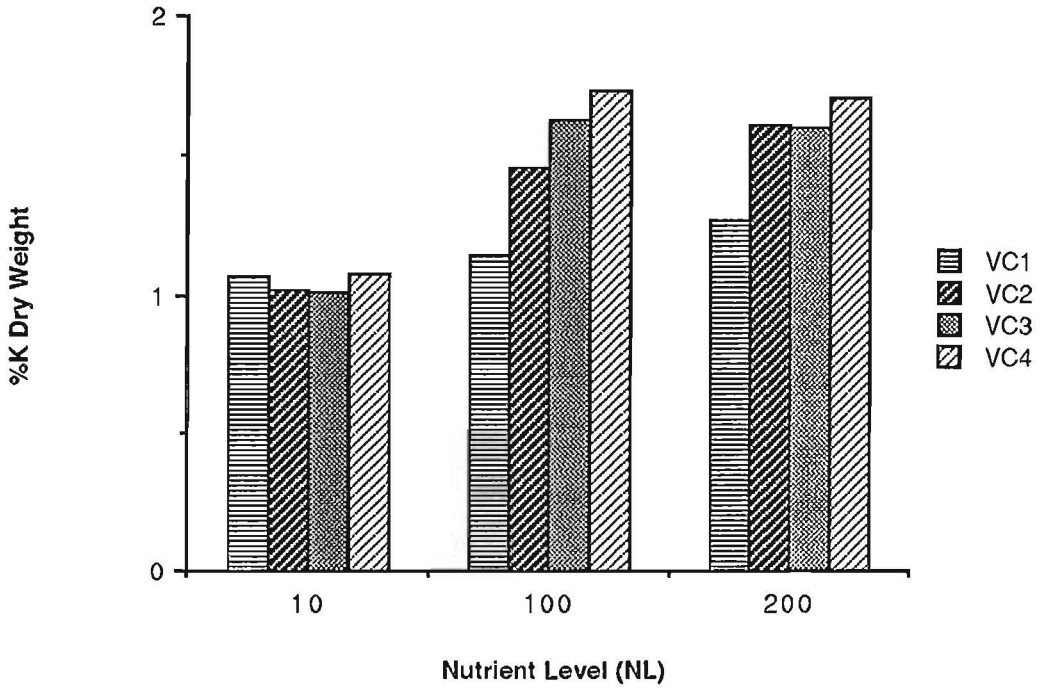


Plate 10.1: Seedling Appearance at NL100

(note suppressed seedling with paler colouration, number refers to N concentration)

Plate 10.2: Seedling Appearance at NL's 5, 10, 100, 200 and 600

(numbers refer to N concentration)

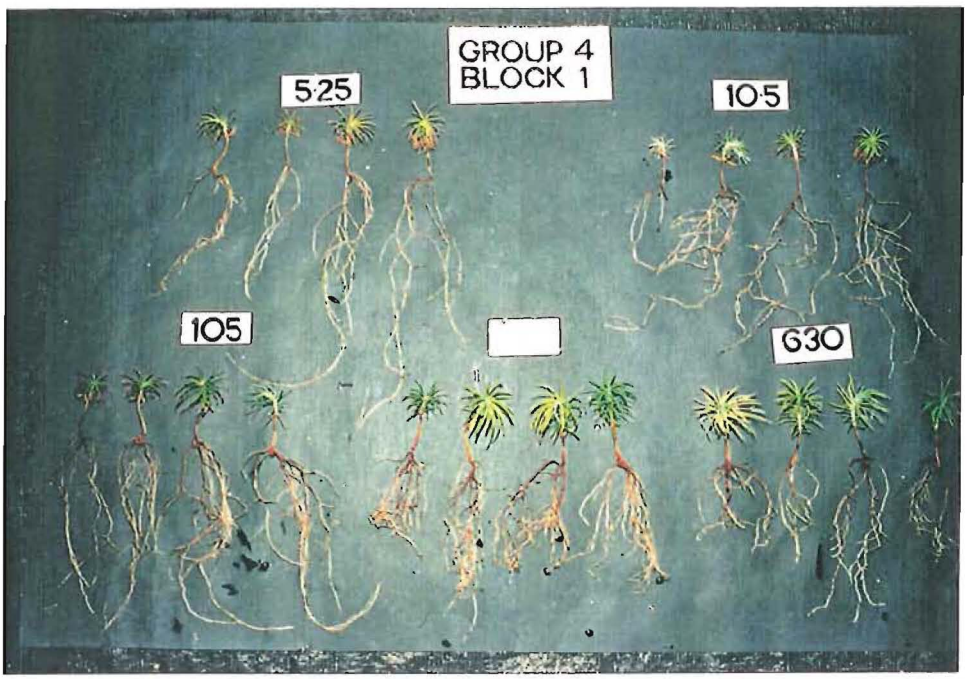


Plate 10.3: Seedling Response to VAM Colonization

(Left; VAM colonized. Right; non-VAM colonized)

CHAPTER XI

INDUCTION AND BREAKING OF DORMANCY/WINTER QUIESCENCE

1. INTRODUCTION

Annual growth of *C. lanceolata* is seasonal in nature; reflecting its adaptation to hot, wet summers when conditions are ideal for vegetative growth, and cooler, dry winters when growth is suspended. Cessation of growth during periods of adverse climatic conditions is an adaptation to permit plant survival (Lavender, 1984). The term "dormancy" is used to describe this state of non growth, and is associated with physiological changes within the plant to withstand such adverse conditions (*e.g.* low temperatures, drought) which would normally result in injury to actively growing tissue. The formation of an over wintering (resting) bud is the most obvious morphological change of dormancy or dormant-like states.

Dormancy is characterised by a series of (gradual) phases which are in turn associated with changes in the environment which serve to trigger physiological changes. As phases are gradual, terminology is vaguely defined and differs between authors (*e.g.* Villiers, 1975; Kramer and Kozlowski, 1979; Lavender, 1984). For the purposes of this study the relationship of growth to phase of dormancy is as given in Kramer and Kozlowski (1979):

1. **Active growth:** Occurs under a wide range of (favourable) conditions.

2. **Predormancy:** Cessation of shoot growth. Range of conditions under which growth occurs narrows. Reversible phase of inactivity, also called prerest and quiescence. Formation of winter buds.

3. **True dormancy:** No growth even under the most favourable conditions.

4. **Postdormancy:** Range of conditions under which growth occurs widens. Growth may still be suspended due to unfavourable conditions. Bud swelling and bud break occur at the end of this phase, leading on to active growth (phase 1).

Phases 2 and 4 are also called relative dormancy or quiescence. At these stages plants are still capable of growth, but growth is suspended by environmental conditions (low temperatures, short day lengths, drought *etc.*). In the case of predormancy, these

environmental conditions also serve to initiate physiological changes such as accumulation of growth inhibitors, lipids and phenols, lignin and starch synthesis, and development of cold hardiness (Villiers, 1975).

True dormancy is where no growth is possible unless the plant is exposed to a certain level of chilling. Chilling appears to breakdown growth inhibitors (Lavender, 1984) and may be an adaptation of the plant to gauge when sub-zero temperatures are less likely to occur. True dormancy is not necessarily exhibited in species which develop over wintering buds. In many warm temperate and tropical species resting buds are formed but can rapidly resume growth when conditions are favourable (Kramer and Kozlowski, 1979; Lanner, 1976), *i.e.* there is no chilling requirement. Where seasonal conditions are such that growth is not possible, buds are said to be in quiescence or relative dormancy (as opposed to true dormancy).

Evidence of shoot phenology from the earlier nursery trial (chapter IV) shows that *C. lanceolata* typically forms a terminal resting bud over winter, and that growth is not resumed until the following spring. This pattern of shoot growth is consistent with Chinese literature and is discussed in chapter XII. Timing of cessation of height growth in species with an indeterminate growth pattern is an essential adaptation for northern woody plants (Hänninen *et al.*, 1990). Trees with relatively late growth cessation may be able to maximise growth in many years, but are also susceptible to damage from early autumn frosts. The environmental trigger that brings about bud formation is not known and the dormancy status (true or relative) of *C. lanceolata* over winter is similarly not known. Three possible environmental conditions are usually associated with induction of dormancy: Short day lengths, low temperatures, and low water availability. The last condition is not likely to act as a trigger in *C. lanceolata* as the nursery trial was carried out in a (comparatively) uniform rainfall environment and with adequate over head watering when soil conditions became dry.

Three timing models (night length, temperature sum, and joint factor) of cessation of growth for northern woody plants were assessed for efficiency by Hänninen *et al.* (1990). None of the models were able to utilise potential growth during all (96) years studied because of large climatic variation; however the night length model, followed by the joint factor model was considered to be the most efficient. In some species it appears that cessation of growth is regulated by joint factors (night length and temperature sum) and this lack of an "optimal" strategy was explained by: i) Different emphasis of traits between those modelled and those present in populations, ii) Natural selection acting on a range of traits so that sub-optimal traits may be present, and iii) adaptation to previous environmental conditions (Hänninen *et al.*, 1990). While the climate in *C. lanceolata*'s distribution in China is less variable than more temperate areas, the issue of dormancy is still important when introducing the species to such areas.

Two experiments were carried out in order to determine the effects of short day length and low temperature on bud formation. A third experiment was made to determine the status of dormancy over winter by subjecting seedlings to various degrees of chilling.

2. GROWTH RESPONSE TO PHOTOPERIOD AND LIGHT INTENSITY.

Growth of many temperate zone plants is strongly affected by daylength (photoperiod); this is because daylength has a pronounced and consistent seasonal pattern. At the equator days are of equal length (12 hours) throughout the year (Kramer and Kozlowski, 1979), sunrise and sunset occur at the same time each day (Salisbury and Ross, 1978). At higher latitudes photoperiod varies according to season; days become longer in summer and shorter in winter (Salisbury and Ross, 1978). While temperature is a major factor in plant distribution it is only broadly related to latitude; daylength, however, is precisely related to latitude (Whatley and Whatley, 1980) and annual variation is consistent.

Where daylength varies greatly (high latitudes) in accordance with temperature seasonality, photoperiod will affect species survival and distribution by regulating plant growth, dormancy, frost resistance, and formation of reproductive structures (Salisbury and Ross, 1978; Kramer and Kozlowski, 1979). *C. lanceolata* occurs at subtropical latitudes where photoperiod does not vary as much as that at temperate latitudes. Nevertheless there is a four hour differential between the longest and shortest day at the northern limit of it's distribution, and this may have an influence on growth. Sensitivity to photoperiod has been observed in some tropical plants, being able to detect slight changes that occur 5 - 15 ^{o} from the equator (Salisbury and Ross, 1978). Shoot growth of some tropical tree species has been shown to increase when grown under days longer than normal (Kramer and Kozlowski, 1979), so it is possible that *C. lanceolata* may be sensitive to photoperiod.

Light intensity can also affect growth, primarily by controlling photosynthesis. Very low light intensity can cause etiolation of leaves (Kramer and Kozlowski, 1979), while high light intensities can cause damage to leaves, especially at seedling stage, by net decomposition of chlorophyll (Kramer and Kozlowski, 1979). Shading of *C. lanceolata* seedlings in other experiments (see chapters IV and VI) was considered necessary in order to produce "healthy looking" seedlings.

In this experiment *C. lanceolata* seedlings were grown under two photoperiods and were also given either 30 % shade or full sunlight in order to determine whether growth was affected by either of these factors.

2.1 Materials and Methods

Seedlings of two provenances were used in this experiment. The seedlings were surplus material from an earlier nursery trial and were three months old. All seedlings were actively growing (*i.e.* no formation of resting buds) at the start of the experiment. Seedlings were grown in commercial potting mix with three month fertiliser. Four treatments representing two light intensities and two photoperiods were used.

2.1.1 Provenance Material. Two provenances representing extremes in north-south distribution of *Cunninghamia* were used: PV1 and PV10. Daylength data calculated from latitudes are given below:

Prov	Latitude	Longest Day	Shortest Day	Difference
PV1	25 ^{o}N	13:34 (hr:mn)	10:26	3:07
PV10	32 ^{o}N	14:06	9:54	4:12

Five pots each with two seedlings from PV10 were used in each treatment, while one pot (160 mm diameter x 120 mm height) containing five seedlings from PV1 was used. Initial size differences between provenances meant that a direct comparison could not be made.

2.1.2 Treatment Conditions. The experiment was carried out over summer (1988-9). All seedlings were grown in a glasshouse with a limited amount of control over temperature. A Campbell Data Logger 21x measured hourly temperature, light and relative humidity for the duration of the experiment. Conditions are as given below:

	mean	day	night
Temperature (^{o}C):	23	26	18
Relative Humidity (%):	74	63	86
Light (μmol m^{-2} s^{-1}):	370	(natural)	

Seedlings were arranged by treatment on two benches (two treatments per bench); the four treatments were:

TR1. Natural daylength, natural light
TR2. Natural daylength,30 % shade
TR3. 8 hour daylength, natural light
TR4. 8 hour daylength, 30 % shade

TR2 and TR4 were grown under frames covered with 30 % shade cloth. The 8 hour daylength for TR3 and TR4 was achieved by placing black polythene sheets over the frames at or around 5.00 pm and removed at 9.00 am the following day. Therefore not

only photoperiod but also the duration of photosynthesising light was also affected by treatment.

2.1.3 Measurements. The experiment was carried out from early December to early April, approximately four months. At the end of the experiment all seedlings were removed and individually measured for basal stem diameter (D), height above ground (H), number of branches (B).

Seedlings were then separated out into leaf (L), stem (S) and root (R) components, oven dried for 72 hours and then weighed. Total weight (T) was obtained by summing L, S, and R. Dry weights of PV10 seedlings were on a per pot basis (two seedlings) while those of PV1 were taken individually for above ground components (stem and leaf) and bulked for roots (due to extensive interwoven root systems). Finally, root to total, leaf to total and leaf to root dry weight ratios were calculated (R:T, L:T, L:R respectively).

2.1.4 Analysis. Analysis of variance (ANOVA) of averaged measurements was carried out using Statview on a Macintosh SE for PV10 seedlings (analysis 1). Individual above ground measurements for PV1 seedlings were also compared (analysis 2). Average root weight and ratios for PV1 are also given for comparison but are not statistically analysed as these were single values (root portions were bulked). The ANOVA format was as follows:

Source	Degrees of Freedom
Treatment (TR)	3
Error	16
TOTAL	19

As mentioned above comparison between provenances is not statistically valid due to different initial size, and different numbers of seedlings per pot.

2.2 Results

2.2.1 Analysis 1 (PV10). Analysis of all measured variables showed no clear or significant differences between treatments at the 95 % level (Plate 11.1). P values of all variables are given in Table 11.1; mean values are shown in Table 11.2.

While there was no significant difference between treatments (Table 11.1), T and R appeared to be greatest at natural daylength (TR1 and TR2). S was greatest under 30 % shade (TR2 and TR4), indicating more stem growth: This is also seen in H and D measurements.

2.2.2 Analysis 2 (PV1). As before there was no significant difference between treatments (P values of all variables are given in Table 11.1; mean values are shown in Table 11.2). B, D, L and S were greatest in TR1, a similar response was seen in PV 10 for L. Other than this there was no overall trend of increased growth response to any particular treatment.

2.3 Discussion

2.3.1 Photoperiod. Results indicate that there is no growth response to different daylengths. This appears not unreasonable as photoperiod is not likely to be a strong environmental trigger at subtropical latitudes. Indeed growth was controlled by temperature for both growth rate (see chapters VI and VII) and cessation of growth, and resting bud formation (see section 3, and chapter IV).

Daylength data for the duration of the experiment and equivalent season at the provenance localities' as well as longest and shortest days are given in Table 11.3. The imposed eight hour daylength in this experiment was almost 2 - 2.5 hours less than the shortest daylengths of PV1 or PV10 and 46 minutes shorter than the natural shortest daylength in Christchurch. If daylength was an important factor in growth regulation, the short eight hour day could well have led to formation of resting buds. Over this same period, seedlings in open conditions (nursery trial) continued to grow until May (one month after the end of this experiment) when bud formation became apparent in some provenances. As there was no bud formation in either provenance in the glasshouse and no difference in dry matter production, it would seem that photoperiod does not affect vegetative growth. In addition it can be seen from Table 11.3 that while the experiment was conducted over summer when temperature was generally warm, natural daylength was in fact decreasing for the majority of the experiment. This indicates that decreasing daylength (and rate of decrease which was greater at Christchurch compared with the provenance localities) does not affect bud formation or growth (although it may affect the rate of growth). It is possible that a photoperiod-temperature interaction may be involved in cessation of growth (Salisbury and Ross, 1978), which would be in accordance with findings for other tree species by Hänninen *et al.* (1990). However in the absence of low temperatures, photoperiod has little or no influence. Daylength may be more important in controlling frost resistance and resumption of growth and is discussed in more detail in chapter VIII and section 4 below.

Irrespective of photoperiod, long term exposure to long days would be expected to produce larger seedlings over those grown under shorter days as a greater amount of photosynthesis and accumulation of photosynthates would result. Height growth of *Pinus taeda* was significantly greater when grown for 15 months under 16 hour days compared with 12 hour days; and for *Pseudotsuga menziesii* under 20 hour days compared with 12 hour days after 12 months (Downs, 1962). It is possible that a longer

duration than in this experiment would have resulted in differences (given favourable growing conditions). However under natural conditions, photoperiod by itself does not appear to be an important factor.

2.3.2 Light Intensity. Light intensity similarly did not affect growth. It is doubtful if the level of shading was enough to reduce photosynthesis as light saturation levels are usually below that of full sunlight. Although the mean natural light level in this experiment was only 370 μmol m^{-2} s^{-1}, even 30 % of this would have been sufficient for quite high levels of photosynthesis to occur; as the light compensation point for *C. lanceolata* is about 20 μmol m^{-2} s^{-1} (chapter VII). However, while no quantitative differences were found, seedling appearance was qualitatively affected; plants grown under shade were dark green in colouration while those under natural light were yellow (see Plate 11.2). This is most likely due to decomposition of chlorophyll (Kramer and Kozlowski, 1979). Photosynthesis of the yellow leaves was probably still occurring at comparable rate to those of the shaded plants, however, as growth was similar.

As mentioned above, shading at the seedling stage was carried out for other experiments. Again, long term effects of prolonged exposure to full sunlight are unknown but the greener colouration of shaded plants suggests that seedling growth is more suited to low light intensities, possibly related to canopy cover.

3. NIGHT TEMPERATURE EFFECTS ON DORMANCY OF SEEDLINGS.

In the previous photoperiod experiment there was no indication that short daylengths had any influence on shoot growth; furthermore while temperatures were conducive to growth, no sign of bud formation was evident under short (8 hour) days. This suggests that temperature is primarily responsible for both controlling the rate of growth and the cessation of growth leading to a dormant state.

The temperature experiments so far have concentrated on rate of growth between different day time temperatures with small day-night differentials, *i.e.* 28/21 °C and 18/11 °C (chapter VI); or large day-night differentials, 28/13 °C and 20/5 °C (chapter VII). In this last experiment the formation of buds and winter colouration in *C. lanceolata* seedlings was noticeable in the lower temperature treatment (20/5 °C). It therefore appears that low night temperatures may be responsible for bud formation and winter colouration; at the lower day but higher night temperature of 18/11 °C no such formation was evident. The aim of this experiment was to observe the effect of differing night temperatures on bud formation in *C. lanceolata* seedlings.

3.1 Material and Methods

3.1.1 Material. Seven-month-old seedlings surplus to the previous temperature experiment (chapter VII) were used. Seedlings were kept in a heated glasshouse prior to the experiment and were actively growing. At the conclusion of the temperature experiment and four days prior to the start of this experiment, seedlings were placed into the two growth cabinets set at 28/13 °C (see chapter VII for conditions); this was to ensure that growth would be promoted. At the start of the experiment conditions were adjusted to those given below.

3.1.2 Treatment Conditions. As bud formation was noted under 20/5 °C conditions but not at those where night temperatures were 11 or 13 °C, two intermediate night temperatures of 7 and 9 °C were chosen. In addition the 15 °C differential between day and night temperatures was maintained in this experiment so as to ensure that day temperatures were not limiting for (potential) growth. Seedlings were placed in two growth cabinets set under the following conditions:

Cabinet (Treatment) 1:

Day conditions	24 °C	60 % RH	16 hours
Night conditions	9 °C	60 % RH	8 hours

Cabinet (Treatment) 2:

Day conditions	22 °C	57 % RH	16 hours
Night conditions	7 °C	57 % RH	8 hours

Relative humidity (RH) was set to obtain a vapour pressure deficit of 12 mbars in each cabinet. 14 seedlings were placed in cabinet 1 and 13 were placed in cabinet 2. Seedlings were watered daily as appropriate to ensure that water was not limiting for growth and/or photosynthesis. After one month in the cabinets seedlings were assessed for signs of dormancy/bud formation and/or winter colouration.

3.1.3 Measurements and Analysis. The experiment ran for one month (April 29 to May 29), at the end of the experiment seedlings were scored for terminal and lateral bud formation. The colour of each seedling was also recorded as either green or brown (winter). Bud formation and seedling colouration were then compared between treatments by Chi square analysis.

3.2 Results and Discussion

By the end of the experiment the majority of seedlings in both treatments had formed terminal buds and were brown in colour. Lateral buds were also formed but were not on as many seedlings. There was no significant difference between treatments for numbers

of seedlings forming terminal or lateral buds, or for winter colouration (Table 11.4). This suggests that night temperatures of 9 ^{o}C are sufficient to induce bud set.

Bud formation leading to bud dormancy can be induced by low temperatures, day length and nutrient and water availability (Villiers, 1975; Kramer and Kozlowski, 1979). In many plant species shortening or short day lengths are the primary signal in inducing bud set, as day length cycles are regular (Villiers, 1975). Similarly, Hänninen *et al.* (1990) found that night length was considered the most efficient model in terms of regulating cessation of growth (in this context day length and night length are conceptually the same). However as shown in this experiment, and in the photoperiod experiment, day (or night) length has no influence on *C. lanceolata* seedlings. Field observations of *C. lanceolata* also attribute winter resting to both low temperatures and water availability (Golfari, 1963) in its natural range in China. As mentioned above, the seasonal temperature climate in subtropical China is less variable than northern temperate (or oceanic) climates. It is therefore possible that seasonal cessation of growth in response to low temperature offers no serious risk of damage by frost; as it would in other climates, where night length or a combination of night length and temperature sum are the normal mechanisms for regulation of bud set.

Hänninen *et al.* (1990) suggested that where regulation of dormancy was not by night length, this may be due to adaptation to a previous environment. As discussed in chapter VIII, *C. lanceolata* can be regarded as a Tertiary relict species whose present distribution has been limited by cooling temperatures.

In this experiment, water and nutrients were readily available and day lengths were longer than experienced in China. These are all conditions that would normally be suitable for growth. Low temperature and specifically low night temperature must therefore be the main environmental stimulus for bud set. In addition, this experiment demonstrates that even short duration of 8 hours per day exposure to low night temperature is sufficient to induce bud set. Height growth of *C. lanceolata* was found to occur at night and cease during the day (Cai *et al.*, 1984) so it is possible that night temperature affects the actual extension growth. Low day temperature was not examined however, so it is not known if this would have a similar effect.

4. WINTER CHILLING REQUIREMENTS OF SEEDLINGS.

Winter chilling is a requirement for most woody species of the temperate zone in order to break dormancy and resume growth in the following spring (Spurr and Barnes, 1980; Lavender, 1984): This requirement ensures that growth does not begin until winter is past (Villiers, 1975). Chilling appears to break bud dormancy by breaking down hormones that inhibit plant growth (Lavender, 1984), and triggering formation of growth

promoters such as cytokinins and gibberellins (Villiers, 1975; Kramer and Kozlowski, 1979).

4.1 Materials and Methods

Between 18 and 19 May, 1989, seedlings which had been raised in a heated glasshouse were potted up into PB $1^1/_2$ bags with commercial potting mix and six month slow release fertiliser, then placed under 30 % shade cloth and naturally hardened off over winter. No seedlings at this stage were actively growing.

4.1.1 Material. Seedlings used in this experiment were from the following provenances: PV's 1 - 3, 5, 9 - 12, representing the latitudinal range. Seedling numbers varied between provenances, treatments and lifting dates and so were pooled for each treatment and lifting date combination.

4.1.2 Treatments. Following potting up, seedlings (comprising treatment 1) were transferred to a heated glasshouse. Weekly observation of these samples were made for bud burst. Seedlings were initially placed under the following conditions (treatments):

TR1	Heated glasshouse (*ca.* 20 °C). PV's 1 - 3, 5, 9 - 12.
TR2	Open ground, subject to frosting. PV's 2, 3, 5, 10, 11.
TR3	Frost free ground (under cloches). PV's 1 - 3, 5, 9 - 12.

Following the first frost, seedlings from each provenance were moved back into the glasshouse from the other two conditions (TR 2 and TR3) at intervals. Lifting times (LT) in weeks since the start of the experiment were as follows:

LT0	22 May, 1989 (start of experiment)
LT2, LT4, LT6	5 June, 19 June, 4 July (two week intervals)
LT9	25 July (three week interval)
LT11	8 August (two weeks)
LT14	29 August (three weeks)
LT16	12 September (two weeks)
LT17	19 September (one week)

Recordings of bud burst were made for each group of seedlings one week prior to transferring to the glasshouse (*i.e.* outside) and weekly thereafter inside the glasshouse. As some seedlings did not have any branches or sub terminal buds, terminal bud burst only was recorded. The experiment was stopped after 20 weeks (9 October) when over 80 % of seedlings in TR1 and over 90 % in TR2 and TR3 had burst bud.

4.1.3 Analysis. As there were varying numbers of seedlings for each provenance three separate analyses were carried out:

1) For comparisons between treatments and lifting times 1, 3, 5, and 7 weeks *after* lifting (designated as 1st, 3rd, 5th and 7th weeks respectively), ANOVA was used. Provenance material was pooled for this analysis. The general linear model was used to account for unequal number of seedlings in each treatment and lifting time. ANOVA format was as follows:

Source	df
Treatment (TR)	2
Lifting Time (LT)	8
TR x LT	16
Error	442
Total	468

2) Provenance differences were assessed within TR1 and TR2+3 separately. For TR1, ANOVA was carried for all PV's at 5, 7, 10 and 15 weeks after the start of the experiment (designated as Weeks 5, 7, 10 and 15 respectively). ANOVA format was as follows:

Source	df
Provenance	7
Error	61
Total	68

3) From analysis 1) it was found that there was no significant difference between TR2 and TR3 (see results). These treatments were therefore combined and analysed for provenance and lifting time variation:

Source	df
Provenance (PV)	7
Lifting Time (LT)	8
PV x LT	56
Error	328
Total	399

4.2 Results

Probability values (Pr > F) for all analyses are given in Table 11.5.

4.2.1 Treatment and Lifting Time Variation. There were highly significant (p = 0.0001) differences in bud burst between lifting times at all times except for the 7th week after lifting. Bud burst was more rapid the later the lifting time (Figure 11.1); this was most clearly shown one week after liftings in later lifting times (LT's 16 and 17) which had between 75 - 100 % bud burst while earlier lifting times had little (2 %) or no bud burst (Table 11.6). This pattern was more pronounced by the 3rd week after lifting; the earliest lifts still had little or no bud burst while intermediate lifts were well into bud burst. By the 5th week most lifts had almost completed bud burst with the exceptions of the earliest lifts (LT0).

There were also significant (p = 0.0107) and highly significant differences between treatments. TR1 was consistently much slower to burst buds compared with TR's 2 and 3. There was no significant difference between TR2 and TR3 (Table 11.6, Figure 11.2). This was most evident in the 7th week where both TR2 and TR3 had completed or nearly completed bud burst while TR1 was only 45 % (final bud burst of 84 % for TR1 was reached by week 18 of the experiment). Very significant (p = 0.0089) and highly significant interactions were seen after the 1st and 3rd weeks respectively.

4.2.2 Provenance Variation Within Treatment 1. There was significant variation between provenances in terms of percentage of bud burst at various times over the experiment (Table 11.7). Week 7 showed the most significant variation (p = 0.013), with PV's 11 and 3 having greater bud burst (at this stage) over PV's 5, 1, and 9. By week 10 most of the provenances had more than 50 % bud burst except for PV's 9 and 10, the two northern provenances. Throughout the experiment PV11 had consistently significantly greater bud burst than PV9; this is graphically shown in Figure 11.3.

4.2.3 Provenance Variation Within Treatments 2 and 3. Significant (p = 0.0376) and highly significant differences were seen in overall provenance variation in all but the first week after lifting. By the fifth and seventh weeks after lifting PV's 9 and 10 had the least bud burst and were significantly less than PV's 1, 11 and 12 (Table 11.8). The overall pattern therefore was similar to that of TR1. Highly significant differences were apparent between lifting times; this has already been given in the first analysis (Table 11.6).

PV x LT interactions were highly significant after the 3rd and 5th weeks and significant (p = 0.0202) after the 7th week. Re-analysing provenance variation by each lifting time showed differences to be significant at LT's 0, 2 (5th and 7th weeks), and 6 (3rd and 5th weeks). Results are shown in Table 11.9.

4.3 Discussion

The results clearly show that chilling and amount of chilling promote more rapid bud burst over non-chilling. Species with chilling requirements vary in the amount of chilling (*i.e.* the minimum length of chilling required to break dormancy); for forest trees this generally ranges from 260 - 2000 hours of temperatures below 5 ^{o}C (Nelson and Lavender, 1979). *Tsuga heterophylla* required 6 - 8 (1008 - 1344 hours) weeks of chilling at 5 ^{o}C with an 8 hour photoperiod and *T. canadensis* required 5 - 8 weeks (Nelson and Lavender, 1979). Some other species reported in Kramer and Kozlowski (1979) are *Pinus sylvestris* (1000 hours) and *Acer saccharum* (over 2000 hours). *Pseudotsuga menziesii* requires 8 - 12 weeks of chilling (Lavender, 1984) while southern species require considerably less; bud break in *Pinus taeda* occurred after only 207 hours but was considerably faster after 1234 hours (Carlson, 1985). This chilling requirement can often limit the southward distribution of northern temperate species as reported for deciduous fruit trees (Kramer and Kozlowski, 1979).

For *C. lanceolata* it is clear that chilling requirement is not a limitation to it's southern distribution in China. As bud burst was in itself not dependent upon chilling (TR1) this implies that *C. lanceolata* does not exhibit true dormancy *i.e.* a dormant state where no growth occurs (even under favourable conditions) and requires exposure to chilling temperatures. However while non-chilling temperatures result in (eventual) bud burst and subsequent growth, even moderate exposure to chilling conditions promotes more rapid bud burst (Figures 11.1 and 11.2). That continued exposure to chilling results in increased rates of bud burst is consistent with other species (*Tsuga heterophylla*, Nelson and Lavender, 1979; *Pinus taeda*, Carlson, 1985) and reflects weakening of dormancy intensity in response to accumulating chilling (Ritchie, 1984). *C. lanceolata* probably has a very low minimum chilling requirement (in order to promote early growth) and so this would have been achieved early on in this experiment (Table 11.7). A similar situation was seen for families of *Pinus taeda* where mean number of days to bud break was 16 - 33 after 207 hours of chilling, 13.4 - 23.3 after 101 hours, and 10.5 - 16 after 1234 hours (Carlson, 1985).

Late lifts (LT's 16 and 17) all burst within one week of being placed under glass, but at the time of lifting no bud burst was evident and seedlings grown in an adjacent nursery trial (chapter IV) showed no sign of bud burst. Similarly, earlier lifts had mostly completed bud burst before the later lifts. Photoperiod was the same for seedling under glass and those outside; therefore warm temperature would have been the trigger for bud burst to occur. Once chilling has been satisfied and dormancy is broken, the time of bud burst is controlled by temperature (Spurr and Barnes, 1980), thus open grown seedlings would have been in the postdormancy phase and would have been capable of growth under favourable temperatures (Lavender, 1984). Temperature sums are considered to be

crucial in regulating development during early spring and summer, and are more efficient in determining timing of onset of growth than night length (Hänninen *et al.*, 1990).

Provenance variation in amount of bud burst is present but appears to be most significant several weeks after lifting of *early* lift times. This is consistent with the above findings as by later lift times chilling requirements would have been satisfied for all provenances. In TR1 differences were most apparent in middle stages (week 7); early stages were all 0 %, while late stages were almost completed. Overall, provenance differences in TR2+3 were similar to TR1. In the first week after lifting PV1 had the least bud burst and was significantly different from all other provenances except PV2; almost all of the bud burst after one week was from later lifts (Table 11.6) LT's 16 and 17.

As interactions were significant from the 3rd week onwards, analysis by lifting time was carried out and provenance differences were found in early lifts (LT's 0 and 2) and in LT6. For LT's 0 and 2 differences were only apparent some time after lifting (5th and 7th weeks), as with TR1 the differences were generally between PV's 9 and 10 (least bud burst) and the other provenances. This would be expected as the early lifts would have received a small amount of chilling, which may have been enough to satisfy most provenances except for PV's 9 and 10 which are more northern and thus subject to colder and longer winters. In LT6 there was no definite trend, but by the 5th week all provenances except for PV2 had completed bud burst indicating that chilling requirements had generally been satisfied.

There appears to be a trend of northern provenances requiring more chilling than southern ones. This is also reflected in timing of bud burst which showed a north-south trend; northern provenances burst bud up to two weeks later than southern provenances (Yu, 1964) when grown at the same (northern) site. Furthermore the overall chilling requirement is very small as bud burst will occur without exposure to chilling temperatures, albeit at a slower rate. As the chilling requirement is slight, all provenances grown outside in natural winter conditions would have satisfied this requirement by spring and would be ready to burst bud under the proper temperature conditions. This could possibly explain why there was no measurable provenance differences in time of bud burst in the nursery trial (chapter IV).

5. SUMMARY

5.1 Photoperiod, Light Intensity and Night Temperature

Quantitative growth measures for both provenances in the photoperiod experiment showed little difference in response to either photoperiod or light intensity. Given the relatively small difference between longest day and shortest day in *C. lanceolata*'s

northern limit, this suggests that photoperiod is not an important factor in limiting the species growth. Seedlings grown under shade were greener in appearance indicating suitability to low light intensities.

Short (8 hour) day length did not induce bud formation under otherwise favourable conditions (for growth). However bud formation was apparent after short duration exposure to low (9 ^{o}C or lower) night temperatures, even with high day temperatures, low water stress and long day length. This suggests that low temperature is the primary trigger for induction of bud formation leading to winter dormancy.

5.2 Winter Chilling

Seasonal growth of most temperate species is characterised by active, predormancy (or initiation of dormancy), true (or deep) dormancy, and postdormancy stages. A requirement for breaking of true dormancy is a level of chilling. Seasonal growth of *C. lanceolata* is similar to that of temperate woody species, including formation of winter buds and subsequent cessation of growth, however there is only a slight chilling requirement for the breaking of winter quiescence in this experiment. Chilling does influence the rate of bud burst (breaking of dormancy), so it would appear that a mild chilling requirement hastens bud burst and subsequent growth.

Differences in requirement are apparent between north and south provenances, but under natural winter conditions (in Christchurch, New Zealand) the chilling requirement for all provenances are satisfied and bud burst is almost immediate when temperatures become favourable.

Table 11.1: Probability (Pr > F) Values

	H	B	D	N	S	R	T	R:T	N:T	N:R
Analysis 1 (PV10)	0.057	0.313	0.268	0.443	0.261	0.103	0.475	0.071	0.160	0.254
Analysis 2 (PV 1)	0.910	0.592	0.862	0.565	0.658					

Table 11.2: Mean Values of Measured Variables

PV	TR	H (mm)	B	D (mm)	N (g)	S (g)	R (g)	T (g)	R:T	N:T	N:R
10	1	108.5	2.7	2.352	1.106	0.266	0.864	2.236	0.388	0.494	1.278
	2	117	2.9	2.550	0.978	0.320	0.942	2.240	0.422	0.434	1.044
	3	111.9	1.7	2.326	0.918	0.282	0.706	1.906	0.370	0.480	1.350
	4	133	2.9	2.608	0.922	0.360	0.724	2.006	0.358	0.462	1.288
	Average	117.6	2.55	2.459	0.981	0.307	0.809	2.097	0.384	0.468	1.240
1	1	116	2.4	2.33	1.010	0.270	0.710	1.990	0.360	0.510	1.420
	2	104.2	0.83	2.10	0.610	0.180	0.460	1.250	0.370	0.490	1.330
	3	118	1.4	2.27	0.740	0.200	0.520	1.460	0.360	0.510	1.420
	4	106	1.4	2.04	0.640	0.180	0.500	1.320	0.380	0.480	1.280
	Average	111.04	1.51	2.185	0.750	0.208	0.548	1.505	0.367	0.498	1.363

Table 11.3: Natural Daylengths (hours:minutes) of Experiment and Provenance Locations

Month	Christchurch	Equivalent Month	PV1	PV10
Mid Dec '88:	15:13	Mid June:	13:33	14:05
Mid Jan '89:	14:49	Mid July:	13:24	13:53
Mid Feb '89:	13:43	Mid August:	12:52	13:10
Mid Mar '89:	12:16	Mid September:	12:09	12:11
Longest Day:	15:14		13:33	14:06
Shortest Day:	8:46		10:27	9:54

Table 11.4: Bud Formation and Winter Colouration of Seedlings Under Different Night Temperature Treatments

	Treatment 1	Treatment 2	Chi Square
Terminal Bud:			
Formed	12 (85.7%)	10 (76.9%)	p = 0.5568
Unformed	2 (14.3%)	3 (22.1%)	
Lateral Bud:			
Formed	7 (50.0%)	5 (38.5%)	p = 0.5466
Unformed	7 (50.0%)	8 (61.5%)	
Colouration:			
Brown	13 (92.9%)	12 (92.3%)	p = 0.9566
Green	1 (7.1%)	1 (7.7%)	

Table 11.5: Probability (Pr > F) Values for Analyses

	1st Week	3rd Week	5th Week	7th Week
Analysis 1				
TR	0.3488	0.0107	0.0001	0.0001
LT	0.0001	0.0001	0.0001	0.4858
TR x LT	0.0089	0.0001	0.8844	0.9087
Analysis 3				
PV	0.8151	0.0118	0.0001	0.0376
LT	0.0001	0.0001	0.0001	0.0081
PV x LT	0.0748	0.0001	0.0001	0.0202
	Week 5	Week 7	Week 10	Week 15
Analysis 2				
PV	0.1886	0.0130	0.0787	0.1065

Table 11.6: Bud Burst % By Treatment (TR) and Lifting Time (LT)

1st Week		3rd Week		5th Week		7th Week	
TR3	22 a	TR3	60 a	TR3	84 a	TR3	96 a
TR2	21 a	TR2	53 a	TR2	81 a	TR2	96 a
TR1	0 b	TR1	3 b	TR1	32 b	TR1	45 b
LT16	98 a	LT16	98 a	LT9	100 a	LT9	100 a
LT17	84 b	LT17	96 a	LT16	98 a	LT11	100 a
LT14	2 c	LT14	92 a	LT14	96 a	LT16	98 a
LT11	0 c	LT11	88 a	LT17	96 a	LT4	98 a
LT9	0 c	LT6	50 b	LT11	93 a	LT14	96 a
LT6	0 c	LT9	45 b	LT4	88 a	LT17	96 a
LT4	0 c	LT4	26 c	LT6	88 a	LT6	95 a
LT2	0 c	LT2	11 d	LT2	86 a	LT2	93 a
LT0	0 c	LT0	0 d	LT0	22 b	LT0	62 b

values in the same column with the same letter are not significantly different at the 95% level.

n.b. 1st week, 3rd week *etc.* refer to observations carried out *after* lifting times (*i.e.* number of weeks under glass).

Table 11.7: Bud Burst % (BB) of Different Provenances (PV) Under Glass (TR1)

Week 5		Week 7		Week 10		Week 15	
PV	BB	PV	BB	PV	BB	PV	BB
11	60 a	11	80 a	11	100 a	11	100 a
3	50 ab	3	80 a	3	90 a	3	90 a
12	40 ab	12	40 ab	5	70 ab	2	90 a
5	30 ab	10	40 ab	2	70 ab	1	80 ab
2	30 ab	2	40 ab	12	60 ab	5	70 ab
10	20 ab	5	30 ab	1	60 ab	12	60 ab
1	10 b	1	20 b	10	50 ab	10	50 b
9	0 b	9	0 b	9	25 b	9	50 b

values in the same column with the same letter are not significantly different at the 95% level.

n.b. Week 5, Week 7 *etc.* refer to actual weeks of experiment (see section 4.1.3)

Table 11.8: Bud Burst % (BB) of Provenances (PV) For TR2+3

1st Week		3rd Week		5th Week		7th Week	
PV	BB	PV	BB	PV	BB	PV	BB
10	25 a	12	65 a	12	96 a	12	100 a
12	23 a	5	63 ab	11	89 ab	1	100 a
11	23 a	3	62 ab	5	88 ab	3	99 ab
5	23 a	11	60 ab	1	87 ab	11	99 ab
3	23 a	9	56 ab	3	85 bc	5	97 abc
9	22 a	1	53 ab	2	76 cd	2	94 abc
2	19 ab	10	51 ab	10	76 cd	9	89 bc
1	13 b	2	49 b	9	57 d	10	89 c

values in the same column with the same letter are not significantly different at the 95% level.

Table 11.9: Bud Burst % (BB) of Provenances (PV) by Lifting Time (LT)

	3rd Week		5th Week		7th Week	
	PV	BB	PV	BB	PV	BB
LT0			12	67 a	1	100 a
			1	20 b	12	100 a
			11	14 b	3	100 a
			2	0 b	11	100 a
			9	0 b	2	90 ab
			10	0 b	5	86 ab
			3	0 b	9	50 b
			5	0 b	10	50 b
LT2			1	100 a	1	100 a
			2	100 a	2	100 a
			3	100 a	3	100 a
			5	100 a	5	100 a
			11	100 a	11	100 a
			12	100 a	12	100 a
			10	33 b	10	67 ab
			9	0 c	9	50 b
LT6	5	100 a	1	100 a		
	12	100 a	10	100 a		
	3	83 a	3	100 a		
	11	50 ab	5	100 a		
	10	33 ab	9	100 a		
	2	30 ab	12	100 a		
	1	0 b	11	100 a		
	9	0 b	2	50 b		

values in the same column and lifting time with the same letter are not significantly different at the 95% level.

Figure 11.1: Bud Burst For TR2 at Different Lifting Times

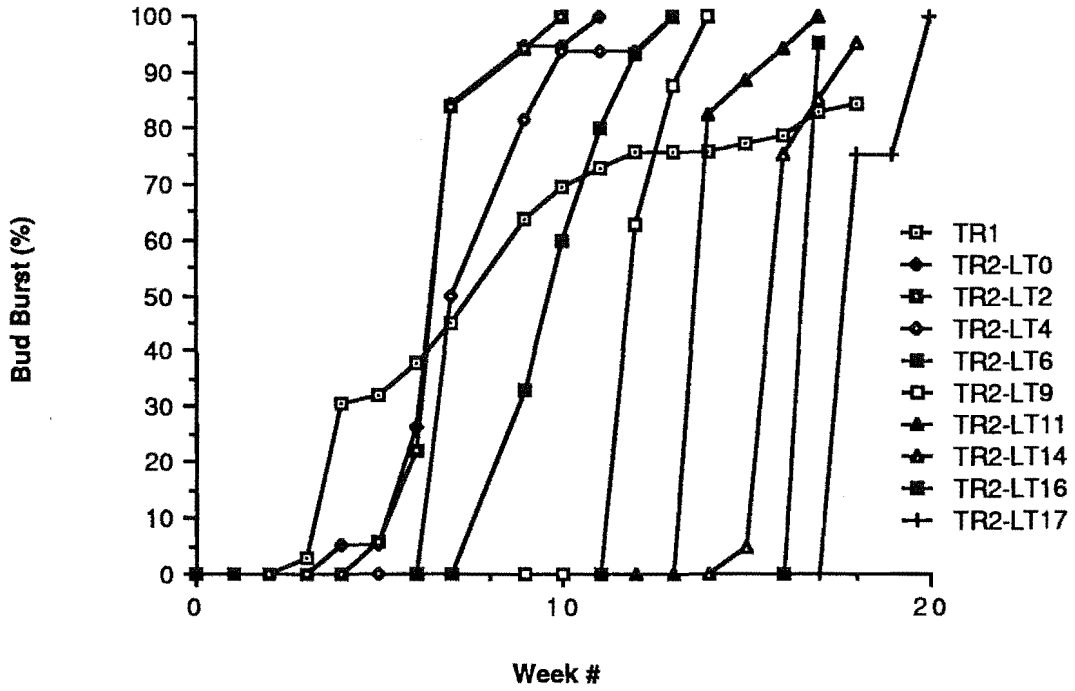


Figure 11.2: Bud Burst by Treatment at Sample Lifting Times

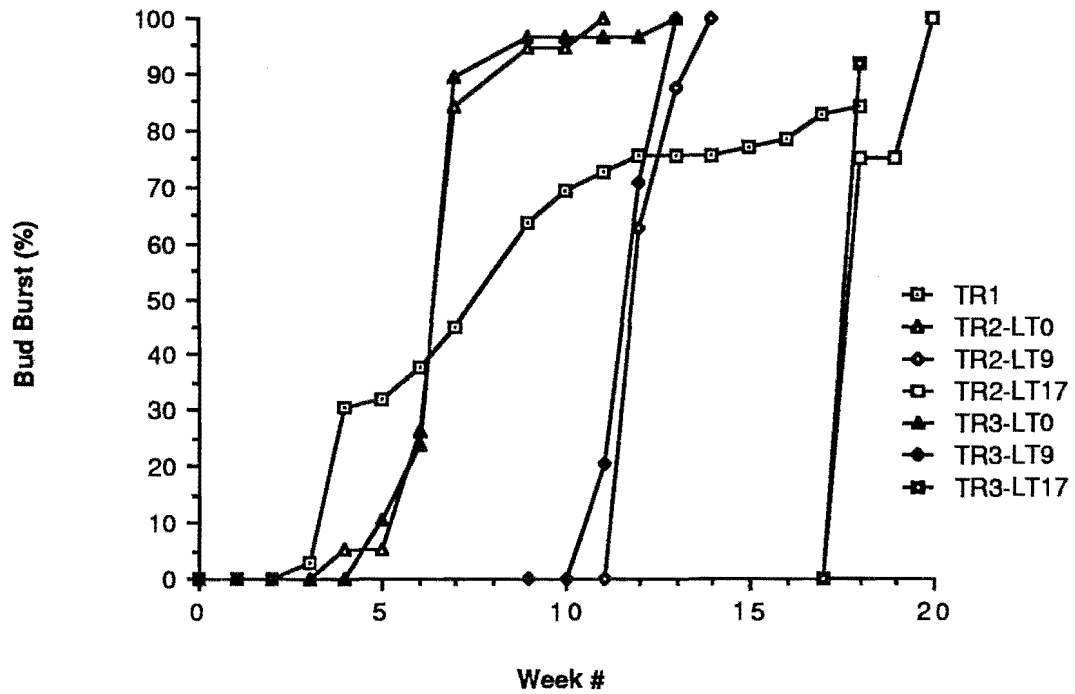


Figure 11.3: Bud Burst ,TR1. Best, Worst and Mean PV's

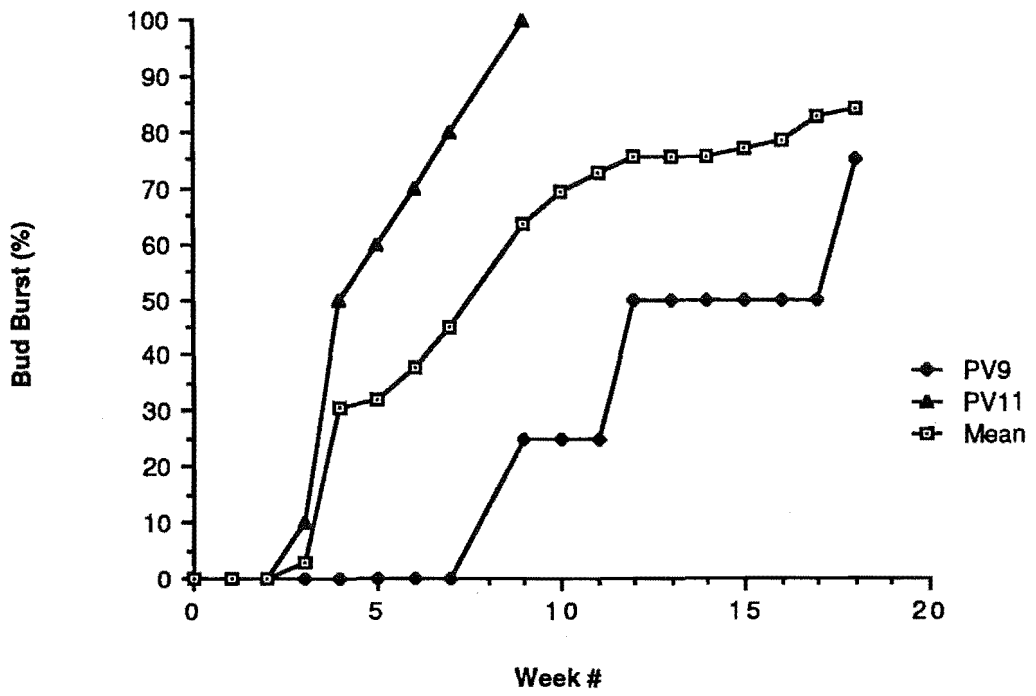
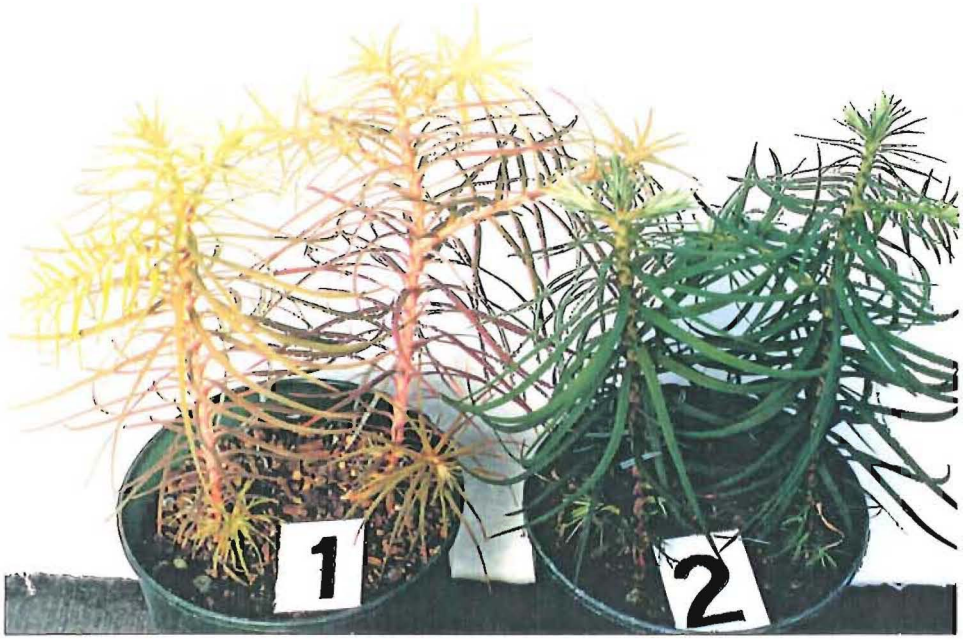


Plate 11.1: Seedling Growth Response to Photoperiod and Light Intensity, PV10

(From left to right: TR1, TR3, TR2, TR4. See text for treatment conditions.)

Plate 11.2: Seedling Appearance Under Natural Sunlight (1) and 30 % Shade Cloth (2)



CHAPTER XII

SEASONAL SHOOT GROWTH PATTERN

1. INTRODUCTION

Shoot growth of most plant species is seasonal. Patterns of annual shoot growth can be characterised as a continuum bounded by predetermined and free growth. Terminology of shoot growth patterns has been confusing with different authors giving different terms for types of growth, the terminology used here will be as described for pine shoot growth in Sweet and Bollmann (1976).

Predetermined growth is typically defined as shoot growth arising from preformed stem units after a rest period (Lanner, 1976; Kramer and Kozlowski, 1979). Growth of this nature is typified by monocyclic pine species which exhibit three sequential phases: (1) initiation of primordia for the next season's growth, (2) dormancy, and (3) extension of the primordia initiated the previous season (Bollmann and Sweet, 1976); *i.e.* in year n differentiation of shoot parts occurs in a resting bud; expansion of these parts then takes place in year n + 1.

Free growth is where simultaneous initiation and elongation of new stem units occurs (Kramer and Kozlowski, 1979). The term is strictly applicable to seedling growth but is also loosely applied to adult growth (Lanner, 1976; Pollard and Logan, 1976; Kramer and Kozlowski, 1979). In some adult pines it appears that stem units at the base of the bud elongate while initiation of primordia occurs at the apex (Sweet and Bollmann, 1976). Thus there is not simultaneous initiation and elongation although the both can occur in the same season without the intervening resting or dormant period.

Purely predetermined growth patterns are evident in many northern temperate species *e.g. Pinus resinosa, P. pinaster* (Lanner, 1976) and species in the genera *Picea, Abies, Tsuga* and *Pseudotsuga* (Cannell *et al.*, 1976). Conversely free growth, or complex polycyclic growth, is characteristic of warm temperate or tropical climates (Bollmann and Sweet, 1976). Still many other species exhibit combinations of predetermined and free growth. In pines at least, growth pattern is an adaptation to the varying climate conditions; predetermined growth enables survival in areas where late or early frosts are a threat, while mild climate conditions favour free growth in order to maximise overall growth (Lanner, 1976).

The growth pattern of *C. lanceolata* has not been studied, at least in the English literature. An understanding of its growth pattern would be of help in assessing its suitability for various climates. While *C. lanceolata* exhibits a definite winter resting bud, suggesting that predetermined growth is a component, the small bud size and its long growing season also suggests that free growth is also present.

2. MATERIAL AND METHODS

2.1 Material

Terminal buds and the preceding season's shoot were collected from first order branches within 1 - 2 m of the tip of the leading shoot (apical bud). Two trees from the experimental plots in Whakarewarewa forest and Longmile, FRI (see chapter XIII), and one tree in a group of three *C. lanceolata* near the Forestry Training Centre (FTC), next to FRI were sampled. Details of the experimental plots are given in chapter XIII, no details were available for the tree near FTC but the tree was smaller in height. Three to five samples were collected from each tree on 1 October 1990. Observations over previous weeks of buds by FRI staff and of arboretum specimens at the Christchurch Botanical Gardens indicated that buds at this stage were fully formed, and swelling prior to bud burst was evident on some trees.

Terminal buds were removed from the samples and placed in FAA solution (for recipe see appendix F). The remaining sample material was labelled and wrapped in plastic bags, samples were then taken back to Christchurch. Terminal buds were placed under vacuum for at least 24 hours to ensure that the FAA solution had been absorbed through the bud tissue (fixed).

2.2 Measurements

Following evacuation of bud material, leaf and leaf primordia counts were made under stereo microscope. As buds lacked scales or scale like leaves there was no distinct morphological division between leaf initials and previous season's leaves. However, after fixing with FAA solution, the leaf initial tissue appears much paler in colour compared with the older leaf tissue and so a visual separation of leaf and leaf initials can be made. The number of sub terminal buds was also counted. Leaf counts were made on the rest of the sample. There were therefore counts made of the following: Leaf primordia (LP), sub terminal buds (SB), old (previous season's) leaves (OL).

An estimate of predetermined growth was obtained by dividing the number of leaf primordia by the number of previous season's leaves. If the proportion obtained is close to one, this indicates that growth is entirely predetermined (arising from initials formed in the over wintering bud); this assumes that both seasons are uniform and also the absence

of ageing effects. Although this is not particularly accurate estimate, this method enabled one collection to be made from a small number of samples (see discussion below).

3. RESULTS AND DISCUSSION

A total of 18 buds from 5 trees were analysed. Table 12.1 shows the resulting proportions (LP/OL). Individual proportions ranged from 0.2072 to 0.6032 but proportions from the same tree had smaller ranges; mean proportions for each tree ranged from 0.2367 to 0.4904. Thus from these estimates less than half of the annual growth on first order branches is predetermined, the remainder is free growth occurring in the growing season.

As mentioned above, the reliability of this estimate must be questioned as the correlation of one season's growth with another is doubtful. Ideally, leading shoots from a number of trees sampled throughout the dormant phase and the subsequent growing season would have given a more precise measure of the proportion of predetermined growth. However the small number of trees available meant that first order branch shoots had to be used, and as the trees were in Rotorua, only one collection could be made, due to limitations of finance.

Predetermined growth is dependent upon genetic and climate factors that affect: i) The number of stem units laid down in year n, and ii) the extent of elongation of these stem units in year n + 1. In the case of i) the number of stem units have been shown to be influenced by water availability for *Pinus resinosa*, and temperature during bud formation for *P. sylvestris, P. strobus* and *Picea spp.* (Kramer and Kozlowski, 1979). In counting the number of primordia laid down in the terminal buds (year n) and comparing this to the previous season's leaves (year n-1) there will obviously be a discrepancy between the climates of the two years. This would give rise to different numbers of primordia being formed for the previous season's growth (year n-1). Thus these results must be regarded as indicative only.

Age and crown position are also important: In trees which exhibit a proportion of predetermined growth, the proportion increases with tree age, in crown position from top to bottom, and from first order to later order branches (Powell, pers. comm.). Being primarily concerned with height growth, first order branch shoots close to the leading shoot were sampled. Trees sampled from the experimental plots were both about 26 years old and were in most likely to be close to a mature growth stage: Height-age curves for Taiwanese *C. lanceolata* showed a decrease in rate of height increase around age 20 years (Liu, 1982). Leaf assimilation rates and biomass production of Fujian *C. lanceolata* indicate stand maturity occurs at 19 - 20 years old (Ye *et al.*, 1984), and CAI and MAI volume curves intersect between 24 and 32 years (Liu, 1982). Therefore buds would

have been likely to have exhibited maximum proportions of predetermined growth in terms of age, but minimal proportions in terms of crown position and branch order.

3.1 Bud Size, Growth Pattern and Growing Season

Resting buds of *C. lanceolata* are typically small relative to the diameter of the shoot. Bud size appears to have a strong relationship to length of growing season (Mitchell, 1964): Species with very small resting buds have a long growth season, characterised by a slow start followed by a moderate even rate; species with large resting buds grow rapidly for a short season.

This is consistent also with predetermined and free growth patterns. Species with predominantly predetermined growth tend to complete growth in a relatively short period (Kramer and Kozlowski, 1979); as growth arises solely from preformed stem units, the resting bud is necessarily large. Species without a distinct resting bud exhibit free growth and thus have no ready made shoot; new shoot tissue is made only when conditions are conducive for growth (Mitchell, 1964). Shoot growth commences slowly compared to preformed shoots as new tissue is made; but can continue to grow as long as conditions permit, hence the longer season (Mitchell, 1964).

The growing season of *C. lanceolata* is relatively long and appears to be similar to the trend identified by Mitchell (1964). In China the growing season at ages 3 and 5 years starts with bud burst and elongation in early to mid April and finishes with bud set around early October to late November (Yu, 1964). Measurements made on trees from age 4 to 7 years showed that growth commenced in early May and finished in late September to late October (Wei, 1981; Cai *et al.*, 1984). The number of frost free (above 0 ^{o}C) days for the provenances used in this study range from 200 to 297 (see chapter IV) indicating that provenance variation does exist in the length of the growing season. This is supported by Yu (1964) who showed small differences in dates of bud burst (up to two weeks) and elongation and large differences in bud set (about 1 - 1.5 months) between provenances. Similarly seedling dormancy timing was found to differ between different areas in Taiwan (Hwang and Sun, 1986).

Nevertheless the overall picture of *C. lanceolata*'s growth season is one that is (under it's natural climate conditions) long. This coupled with the small sized bud suggests that the growth pattern has a minor predetermined component and a subsequent major free growth component.

3.2 Growth Pattern and Climate

In comparing *C. lanceolata*'s growth pattern with those of pines, the most similar pattern is the elliotii/echinata pattern: The annual shoot is elaborated by both free and fixed (predetermined) growth, and the free growth components constitute a significant part of

the annual shoot (Lanner, 1976). As mentioned above the nature of the growth pattern is related to the environment. The elliotii pattern allows advantage to be taken of an environment with long growing seasons separated by short, frosty winters; by combining both types of growth the tree is buffered against unfavourable years (Lanner, 1976).

Long growing season and short winters are also a characteristic of the environment of *C. lanceolata.* The winter while quite mild in the southern most distribution of *C. lanceolata* (*e.g.* Guangdong, Yunnan, Fujian) is associated with comparatively dry conditions (Watts, 1969). A combination of cold and dry conditions then necessitates a dormant period, enabling formation of part of the next season's shoot within the bud.

Adaptation of a species to long growing seasons and its resulting growth pattern has disadvantages when transferring the species to a different environment. If the new environment is colder, then early or late frosts can be a problem, at least at the seedling stage. This has been demonstrated for *C. lanceolata* in the nursery trial (chapter IV) where spring frosts killed growing tips that had recently burst bud, and autumn frosts killed growing tips that had failed to form buds. Because control of timing of bud burst (through chilling requirements) and bud set are genetic, frost damage is likely to be a major limitation to successful establishment here in New Zealand. However selection of northern provenances with shorter growing seasons (*e.g.* provenances from Anhui, Zhejiang; Yu, 1964) may overcome early (autumn) frost damage.

4. SUMMARY

Leaf primordia counts taken from first order branch bud samples of 26 year old trees were compared with the previous season's growth. Results indicated that predetermined growth was a relatively minor component in terms of the annual shoot growth, the remainder was free growth. The growth pattern appears to be similar to the elliotii pine pattern suggested by Lanner (1976) and this is supported by Chinese data in terms of length of growing season. Bud size is small and this coupled with the long growing season implies that predetermined growth is indeed a minor component.

As length of growing season is genetically controlled, the placement of *C. lanceolata* in New Zealand environments with early and late frosts can cause significant frost damage during the seedling stage. Selection for provenances with shorter growing seasons may reduce autumn frost damage.

Table 12.1: Terminal Bud Leaf Primordia Counts and Preceding Season's Growth

Tree	Bud #	LP	SB	OL	LP/OL
WF1	1	53	5	165	0.3212
	2	83	3	209	0.3971
	3	59	4	211	0.2796
	4	81	5	203	0.3990
	mean	69	4.25	197	0.3502
WF2	1	84	5	226	0.3716
	2	107	5	207	0.5169
	3	114	5	189	0.6032
	mean	101.7	5	207.3	0.4904
LM1	1	134	4	453	0.2958
	2	130	4	431	0.3016
	3	121	5	432	0.2801
	mean	128.3	4.33	438.7	0.2925
LM2	1	92	5	444	0.2072
	2	90	6	339	0.2655
	3	102	7	417	0.2446
	mean	94.7	6	400	0.2367
FTC	1	118	3	292	0.4041
	2	121	5	253	0.4783
	3	139	7	479	0.2902
	4	114	6	271	0.4207
	5	152	5	320	0.4750
	mean	128.8	5.2	323	0.3988

Notes LP: Terminal Bud Primordia (First Order Branch)

SB: Sub-terminal Bud

OL: Previous Season's Leaves

CHAPTER XIII

WOOD PROPERTIES OF NEW ZEALAND GROWN *Cunninghamia lanceolata*

1. INTRODUCTION

Following an extensive appeal for information on New Zealand grown *C. lanceolata*, three stands (plots of more than two or three trees) of the species were found to exist. The largest stand is located in New Plymouth while the remaining two plots are in Rotorua; details of the stands are given below. Another (ornamental) plot of five trees is located in the Eastwood Hills Arboretum, Gisborne, but was not analysed in this study.

That *C. lanceolata* has been grown in New Zealand, albeit on a very small scale, demonstrates to some degree that climate, at least in these two areas, is suitable for the species. Wood properties of a species vary with a number of factors *e.g.* site, climate, geographic location, genetic origin *etc.* (Haygreen and Bowyer, 1982). However, as there are known stands of *C. lanceolata* of varying ages it was seen as appropriate to get some preliminary information on wood properties.

All three stands were visited on 7 and 8 June 1989; core samples and heights and diameters were taken. Following this a second visit to the New Plymouth stand was made on 16 January 1990. Sample trees were felled and wood samples were removed for detailed analysis of the physical, mechanical and drying properties. As there were limited numbers of available trees, not all properties could be tested. The tests carried out were standard tests and concentrated on fundamental aspects. Results should be considered as indicative only; details of tests are given below.

Wood properties give an indication of suitable end use; in China and Taiwan the species is used extensively for buildings (light structural and flooring), coffins, and poles, boat building, furniture and cabinet work, boxing and crates (Ko, 1958; Dallimore and Jackson, 1931; Chun, 1921; Liu, 1982). It is also used in particle board construction (Liu, 1982; Chen, 1984; 1987) and in structural glue-laminated timbers (Liu and Lin, 1986). While seemingly not widely used *C. lanceolata* is also suitable for sulphate (kraft) pulps, based on experiments in both Taiwan (Liu, 1982; Ku *et al.*, 1987) and Brazil (Foelkel *et al.*, 1978; de Lelles *et al.*, 1978).

2. MATERIALS AND METHODS

2.1 Material

Camp Huinga, New Plymouth (CH): This stand comprises some 112 trees in an approximate area of 40 m x 25 m (0.1 ha); stocking is therefore around 1100 stems per hectare (Plate 13.1). It was thought that the stand was established around 1931; the seed source is unknown. Previous plot work on this stand had been carried out in January 1989 by Groome Pöyry Ltd (K. Buck, pers. comm.) and consisted of diameter measurements of 46 trees (nearest to the middle of the plot) and height measurements of three trees.

On the first visit diameter measurements of a further 54 trees, and heights of a further 12 trees (chosen at random) were taken. Twenty trees were then chosen at random from the 100 which had been measured, and two 5 mm diameter cores were extracted from each tree. The cores were taken at right angles to each other at breast height (1.4 m) using a 5 mm increment borer. The cores were marked and placed in plastic straws and taken to FRI, Rotorua for analysis. Five representative trees from an adjacent stand of *Cryptomeria japonica* of similar size, area and stocking were also measured for diameters and heights.

On the second visit five trees were selected at random and felled. Heights were recorded and discs were taken from the butt, at breast height (1.4 m) and at three metre intervals up the trees. A one-metre bolt was removed from each tree at breast height. Bolts and discs were then taken back to FRI, Rotorua for further breaking down and analysis. Disc material was used for analysis of *physical properties*, while the bolts were sawn to produce specimens for analysis of *mechanical properties* and *drying properties*.

Whakarewarewa Forest, Rotorua (WF): This stand comprised part of a compartment trial established in 1964 to evaluate several species. The seed source was from Taiwan. Diameters of 30 trees were measured and heights were taken of ten of these. Increment cores were taken from seven randomly selected trees.

Longmile GTI Block, Rotorua (LM): Also established in 1964 from Taiwan seed (possibly the same), this stand comprised 12 trees only (Plate 13.2). All trees were measured for diameters and heights. In addition two trees were randomly selected and felled and discs from the butt, 1.4 m, 3 m, 6 m and 9 m were taken for sectional analysis of wood properties.

Stand measurements are summarised in Table 13.1. Measurements of the sample trees at Eastwood Hills Arboretum are included as the trees are of similar age to those at Camp Huinga.

2.2 Sawing Pattern

Bolts from the Camp Huinga trees were broken down according to the pattern shown in Figure 13.1. The (centre) diametral plank was sawn to produce 1 m long side-matched specimens for green and air-dry testing of **mechanical properties**. Specimens were further sawn to 20 mm x 20 mm finished dimensions. These specimens were then sawn to produce small clear samples for three mechanical tests, the dimensions of the samples are given under the relevant tests for mechanical properties.

Planks either side of the centre plank (labelled "north" and "south") were next sawn to produce specimens for evaluating **drying properties**. The 1 m planks were broken down to two matching sections with dimensions of 60 mm x 60 mm. These were then sawn in half to give two samples of 480 mm x 60 mm x 60 mm per section. A diagrammatic representation is given in Figure 13.2.

2.3 Analysis

Analysis was carried out at the Wood Technology Laboratories at FRI, Rotorua.

Physical: Discs were measured for diameter over and inside bark, and diameter of heartwood. They were then divided into sample sectors of either 5 or 10 growth ring sections or heartwood and sapwood sections. Green weights and volumes of sector samples were recorded, sector samples were then oven dried at 105 ^{o}C for 24 hours. Oven dry weights and volumes were then recorded. Those discs taken at a height of 3.0 m up each tree were further sectioned and analysed for dimensional shrinkage: Longitudinal (Lon), radial (Rad), and tangential (Tan).

Data were then entered into the FRI VAX computer and run through a program to calculate green and basic densities, moisture content, and volumetric shrinkage for each section; and weighted means of these parameters for each disc. Another program was then run to calculate cumulative volumes, heartwood present, and densities for each tree. Parameters calculated are defined as per Harris (1986) and Haygreen and Bowyer (1982):

Green Density (kg m^{-3}) = (weight of fresh sample / volume of fresh sample)

Basic Density (kg m^{-3}) = (weight of oven dry sample / volume of fresh sample)

Moisture Content (%) = [(green density / basic density) x 100] -100

Volumetric Shrinkage (%) =[(volume of fresh sample - volume of oven dry sample) / volume of fresh sample] x 100

Core samples were divided into sections of approximately 5 rings or >30 mm whichever was the longest. Basic densities were derived using the maximum moisture content method (Smith, 1954).

Drying: A total of 48 samples from the five trees were obtained for testing. Samples from the matched sections were either placed in an FRI experimental kiln under a conventional radiata kiln drying schedule (70/60 °C dry/wet bulb temperatures), or allowed to air dry. Weights of samples were recorded and when samples had reached a constant weight, or were decreasing by small amounts, the samples were removed and placed in an equilibrium moisture content (EMC) chamber set at 12%.

After the kiln-dried samples had been been in the EMC chamber for 74 days and air dried samples for 9 days; radial (Rad_{trt}), tangential (Tan_{trt}), and volumetric (Vol_{trt}) shrinkage were measured. Samples were then cut into sub-samples to determine moisture contents; the centre sub-samples were then steamed for 4 hours and placed back in the EMC chamber to assess recovery (Rad_{rec}, Tan_{rec}, and Vol_{rec}) from shrinkage. Drying curves and shrinkages were calculated for both treatments, as well as a visual assessment for degrade (*e.g.* collapse, checking, distortion *etc.*).

Mechanical: Small clear specimens were taken to the University of Canterbury and three mechanical tests were applied: Static bending, compression parallel to the grain, and shear parallel to the grain. Modulus of elasticity (MOE), modulus of rupture (MOR), fibre stress at the proportional limit (FSPL), maximum compression strength (MCS), compressive strength at the proportional limit (CSPL), and maximum shear strength (MSS) were all calculated from the above tests. The tests were carried out on an Instrom 1195 universal testing machine. Nominal density at the time of testing, basic density, and moisture content at time of testing were calculated. Preparation of samples and methods were as per British Standards no. 373-1957, with slight modification to rates of crosshead movement; further details are given in Walford (1985).

Anatomical and Pulping: These aspects were beyond the scope of this study; however there have been several studies on these aspects. Summary findings are tabulated and discussed below.

3. RESULTS

3.1 Physical Properties

Table 13.2 shows cumulative log volumes and densities for each whole tree. The means of each stand are also shown. Younger trees from LM clearly have a greater moisture content then those from CH. This is reflected in heavier green densities (and slightly lighter basic density) in the LM stand. Reduction in moisture content with age is due to

increased heartwood formation as a general rule (Cown and McConchie, 1982; Zobel and van Buijtenen, 1989) and this is also the case for *C. lanceolata* .

Weighted means of disc densities, moisture contents and volumetric shrinkage by position in the tree are shown in Table 13.3 and Figures 13.3 - 13.5. Between tree variation is quite large (Figures 13.3 and 13.4), but there is a general trend of high densities and moisture contents at the butt which drop quickly further up the tree, then level and then begin to increase with further height up the tree. Shrinkage does not appear to follow this trend but remains relatively uniform throughout the tree.

Core samples from breast height were used to show radial variation of basic density. Average values from WF and CH are shown in Figure 13.6. A similar trend as seen in variation along the tree log is evident. Mean basic density of core samples from the 20 CH trees was 327 kg m^{-3} (with a range of 276 - 412 kg m^{-3}). This was similar to the mean basic density of the five, randomly selected, CH trees felled for further analysis (322 kg m^{-3}, range of 297 - 348 kg m^{-3}). It is likely then, that these trees are indicative of the stand as a whole.

Dimensional shrinkage is summarised as disc weighted means in Table 13.4. This appears to be more consistent between trees, and volumetric shrinkage is comparable to those values obtained by the previous disc sections (differing by only 1.2 % or less). There was little variation in shrinkage according to radial position, further emphasising the uniformity of this property.

3.2 Drying Properties

Figure 13.7 shows drying rates of both kiln dry and air dry samples based on mean moisture contents. A comparison with "typical" *P. radiata* drying rates in a conventional kiln schedule using 100 mm x 50 mm x 600 mm specimens is given in Figure 13.8 (data from NZFS, FRI, 1974). A comparison of drying times between air and kiln drying to 60 % mc is shown in Table 13.5. Drying times to lower moisture contents are given for the kiln dried material only as many air dried samples had not fallen below 30 % (approximate fibre saturation point).

A visual estimation of degrade was made; only two kiln dried samples showed very slight collapse in the sapwood and these were negligible over the entire sample dimensions. This would indicate that at these drying schedules *C. lanceolata* is relatively stable. Steaming following drying (reconditioning) is used to aid recovery from possible collapse (Clifton, 1990); if degrade has occurred steaming may reverse this by causing enlargement in dimensions. Volumetric shrinkage is given in Table 13.6 and where possible, dimensional shrinkage is also shown: As samples were not truly flat sawn only

a proportion of the samples could be measured for dimensional shrinkage. Final shrinkage following recovery after steaming are also included.

3.3 Mechanical Properties

Mean results of all three tests are given in Table 13.7. Because of the small sample size of 36 specimens per test (and 72 for shear) analysis by radial position (or cambial age) or tree side (east or west) has not been carried out.

Raw data for mechanical and drying properties are given in appendix G.

3.4 Anatomical and Pulping Properties

Summary results from various authors are presented in Table 13.8.

4. DISCUSSION

4.1 Comparison With Other Exotics

Table 13.10 shows comparative data for four New Zealand grown exotic species, *C. lanceolata* data is from the CH stand only. There is very little data available for *Cryptomeria japonica*; the data obtained is from Duggan (1983) and represents the mean of only nine samples (number of trees unknown). Whole tree basic density is similar to *Sequoia sempervirens*, although low in comparison with other conifers (Young, unpubl.). In general *C. lanceolata* has "lower" wood properties than *P. radiata* at air dry or oven dry levels; green values are more comparable. *C. lanceolata* is slightly heavier than *Cryptomeria japonica* and this is reflected in a larger MOE. Dimensional shrinkage is similar for all four species and is small in comparison to many other conifer species.

From the mechanical properties in Table 13.9, *C. lanceolata* is not as strong as *P. radiata* and this is almost certainly due to the much lower basic density of the species: Generally density is closely correlated with most mechanical properties (Haygreen and Bowyer, 1982) and this is the case with *C. lanceolata* (Liu, 1982). It would therefore be unsuitable for framing; however in other properties such as shrinkage and ease of drying, it is very similar to *P. radiata*. Durability (heartwood resistance to fungal attack) was not tested as this is a long term measure; the standard test is to rate heartwood test stakes in ground contact over a number of years (Harris, 1986; Keating and Bolza, 1982). *C. lanceolata* is considered to be durable in China and Taiwan (see below). *Sequoia sempervirens* is considered moderately durable when grown in New Zealand (Clifton, 1990) and highly resistant to decay in North America (Haygreen and Bowyer, 1982) so it is possible that *C. lanceolata* grown in New Zealand will be durable but may not be as durable as the Chinese timber.

As it demonstrates little or minimal degrade and appears to be relatively stable it could be used in non-structural situations such as weather-boarding, panelling, joinery or finishing.

4.2 Comparison With Chinese Grown Trees

Wood properties are affected by both environment and (genetic) seed source. Although it can be difficult to separate the components, often there is a large interaction (Zobel and van Buijtenen, 1989). When grown as an exotic (*i.e.* in a different environment), a species will almost certainly have different wood properties. This has been documented for both tropical and temperate conifers such as *Pinus caribaea, P. taeda, P. contorta, P. sylvestris* (reported in Zobel and van Buijtenen, 1989). New Zealand grown *Sequoia sempervirens* has generally much lower density and mechanical strength than Californian material (Clifton, 1990).

C. lanceolata also appears to follow this pattern. Basic densities of Chinese/Taiwanese grown material range from approximately 300 to 490 kg m^{-3} (Ye and Zhang, 1987; Chang and Duh, 1988; Chen, 1962; Chiang, 1967; Liu, 1982; Mashita, pers. comm.) and *C. konishii* a Taiwan species morphologically very similar to *C. lanceolata* has high basic densities of 410 to 450 kg m^{-3} (Keating and Bolza, 1982; Mashita, pers. comm.). This compares with basic densities of 329 kg m^{-3} for Brazilian *C. lanceolata* (de Lelles *et al.*, 1978) and 339 kg m^{-3}, of the Camp Huinga material which is most likely to be of older age than the Chinese material, which is usually harvested well before age 58 years (samples in Liu, 1982, were up to 36 years and 35 years in Chang and Duh, 1988) and hence has a greater density due to more heartwood formation and more dense outerwood. Volumetric shrinkage (Table 13.4) is slightly greater than 8.2 % reported by Chen (1962).

In terms of mechanical strength Taiwanese *C. lanceolata* has MOE's of between 7.5 and 10.3 GPa (Liu, 1982) while Chinese material has MOE's of 6.6 - 10.6 (Lin *et al.*, 1984), which are comparable to that of *P. radiata* (Table 13.8). Camp Huinga material had an average MOE of 7.4 GPa, again demonstrating the difference. Other comparisons are given in Table 13.9: Basic density and MCS are similarly greater in Taiwanese and Chinese grown *C. lanceolata* than the New Plymouth material and comparable to *P. radiata*. Initial spacing and thinning can significantly affect *C. lanceolata's* physical properties. Tracheid length ring width, latewood percentage, basic density and shrinkage were all found to be affected by spacing and thinning (Xiong, 1987); this subsequently affected mechanical properties such as compressive strength, MOR and MOE. Similarly mechanical properties MOR, MOE, MCS, and IBS (impact bending strength) are highly correlated with specific gravity; correlation coefficients range from 0.73 to 0.93 (Shi *et al.*, 1987). It must be remembered that the wood properties are strictly only indicative of that site (New Plymouth), seed source (unknown), and tending regime, and a broad

extrapolation must be made with caution. However it appears from these results that New Zealand *C. lanceolata* may well have generally less desirable wood properties than its Chinese/Taiwanese counterparts. In this respect it is similar in response to other species such as *Sequoia sempervirens* and *Pinus taeda* (Clifton, 1990; Harris, 1986; Haygreen and Bowyer, 1982).

It does not appear that durability tests have been carried out, although the wood is referred to as "durable" (Dallimore and Jackson, 1931; Chun, 1921) and "moderately durable" (Ko, 1958; Chiang, 1967). Buried timber (over 200 years) in China has been reported to be in an excellent state of preservation (Chun, 1921). *C. lanceolata* is used in joinery due to its durability and stability (NZFS, 1985). Keating and Bolza (1982) give a durability rating of 1 (greater than 25 years) for *C. konishii* so it would seem that the heartwood could be used in exterior situations.

Durability depends upon the type and amount of fungitoxic extractives within the tree (Haygreen and Bowyer, 1982). A number of studies have been carried out to determine extractive components (Shieh *et al.*, 1977; Lee, 1982; Lu and Wang, 1986; Chang and Duh, 1988) and their effects on microbial activity (Lu *et al.*, 1987; Shieh *et al.*, 1986; Shieh *et al.*, 1987; Wang *et al.*, 1989). Cedrol is the major extractive component of the 39 found in *C. lanceolata* (Lu and Wang, 1986) and it appears that it also is the main component conferring natural resistance to termite and fungal attack (Lu *et al.*, 1987). Total extractive content of 35 year old *C. lanceolata* in Taiwan was 23.9 % for heartwood and 14.4 % for sapwood (Chang and Duh, 1988) which is relatively high. Generally, extractive content ranges from under 3 % to over 30 % of oven dry weight (Haygreen and Bowyer, 1982) and in *P. radiata* from 2 - 9 %, typically 2 - 3 % (Lavery, 1986).

4.3 Variation Across a Radius and With Height in the Stem

Radial variation in wood properties shows a very clear pattern for green and basic densities. Figure 13.6 shows radial variation at breast height (1.4 m) and this is similar for all other heights sampled by disc sections. There is an initial high density around the core which then rapidly drops away from the centre, density then increases towards the outside. Moisture content is not shown but in all cases there was a direct increase in moisture content from the centre to the outside.

It is possible that resin deposition (extractives) occurring at the centre or heart of the tree accounts for the initial high densities as has been attributed in other species (Young, unpubl.; Zobel and van Buijtenen, 1989), although other changes such as earlywood-latewood transition can also account for this. Thereafter the increase in density is consistent with a change from juvenile to mature wood (Zobel and van Buijtenen, 1989; Wang and Tserng, 1987). The increase in moisture content away from the pith is probably also due to heartwood formation. Extractive (terpenes, polyphenols, inorganic

compounds *etc.*) content affects densities as heartwood formation around the pith may contain a higher proportion of extractives (Haygreen and Bowyer,1982; Uprichard, 1963). In Chinese grown trees, specific gravity at breast height increased rapidly away from the pith and stabilised at the 13th - 18th rings (Ye and Zhang, 1987).

Variation in tracheid length has been studied by a number of authors. Radial variation showed a consistent pattern of increasing tracheid length from the pith outwards, reaching a maximum between the 10th and 15th ring (Cai and Liu, 1986; Lu, 1985); length thereafter declined (Cai and Liu, 1986) or undulated (Lu, 1985). Wang and Tserng (1987) found increasing tracheid length up to the 12th ring, in subsequent rings length was constant. This is similar to findings by Ye and Zhang (1987), where tracheid length, like specific gravity, increased up to the 13th - 18th ring before stabilising. Differences in tracheid shape between early and late wood are apparent (Chiang, 1967; Lu, 1985) and also between juvenile and mature wood (Wang and Tserng, 1987; Li *et al.*, 1988).

Variation with height, as mentioned above, also shows a similar pattern to radial variation. This pattern has also been reported for *Chamaecyparis obtusa* and *Tsuga heterophylla* in Zobel and van Buijtenen (1989). The conventional pattern is that of decreasing basic density with increasing height, due to a greater proportion of juvenile wood; unless there is little difference between juvenile and mature wood, in which case there is little change.

Studies of tracheid length have shown an increase up to mid stem (10.3 m) thereafter decreasing to the crown (Wang and Tserng, 1987). Similarly Cai and Liu (1986) found a slight increase with height up to 9.3 m (total height unspecified), which then decreased. Tracheid length is important in affecting quality of fibre based products (pulp and paper) rather than mechanical properties (Lavery, 1986). It also affects longitudinal shrinkage during drying, although in practical terms this is usually the smallest component of shrinkage and the least important.

Extractive content was not examined in this study; it would be useful to determine extractive contents as they can affect densities (both radially and in height) and hence have a bearing on the density / strength relationship. Variations in the components and total amounts of extractives influence resistance to fungal attack, as has been shown in both (native) North American and New Zealand grown *Sequoia sempervirens* timber. High extractive contents reported in a study on kraft pulping of Brazilian grown *C. lanceolata* (10.7 %) by de Lelles *et al.* (1978) and in heartwood from Taiwan (23.9 %) by Liu (1982) suggests that a large amount of extractives would be expected in New Zealand grown timber (see sections 4.1 and 4.2 above).

4.4 Drying Rates

From Figure 13.7 and Table 13.5 it is evident that kiln drying is a much quicker and more controllable process then air drying. Final drying time to equilibrium moisture content is not known for air dried samples, but at 60 % mc time spent in the kiln was already one tenth of that required for air drying. As there was minimal degrade in either of the schedules it would seem that *C. lanceolata* can be easily kiln dried at conventional *Pinus radiata* schedules; economics permitting. Unfortunately it was not possible to carry out a high temperature schedule so it is not known if any significant degrade would occur at these temperatures.

Drying rates in the conventional schedule are very close to those of *P. radiata.* Although the *P. radiata* samples reported here have different dimensions it is sufficient to demonstrate the similarity (Figure 13.8). Drying times for other species are given by way of comparison: Treated *P. radiata* of 50 mm thickness takes approximately 10 - 18 days to dry; untreated material between 4 - 8 days. Untreated pine species with "wet" heartwood and partly air dried *Sequoia sempervirens* (25 mm thickness) take 8 - 10 days; green *Sequoia sempervirens* (25 mm thickness) takes 14 - 18 (Kininmonth and Williams, 1974). The first *C. lanceolata* samples were dried by day 8 and most were dried by day 11, well within the drying time for treated *P. radiata* and green *S. sempervirens*, and similar to "wet" heartwood pines and partly air dried *S. sempervirens.*

Shrinkage (from drying to 12 % MC) is comparable to both *P. radiata* and *Sequoia sempervirens* (Table 13.10). No Chinese data were available, but shrinkage was considered as very little by Chiang (1967); shrinkage was also less than *Cryptomeria japonica* and *Taiwania cryptomerioides* (Wang, 1989). Drying schedules have been developed in Taiwan including press drying (Jai and Lee, 1987; Hsiung, 1986). Steaming was carried out in order to see if recovery was possible in the slightly collapsed samples; all samples were steamed to assess any changes in dimensions (Table 13.6). As the air dry samples were still drying it can be seen that shrinkage was still occurring (as evidenced by small changes in dimensions) and as a result steaming did not produce any recovery. Final results are comparable, however, to those of the kiln dry schedule indicating that air dry samples would have been very near to equilibrium moisture content.

4.5 Pulping Studies

Pulp yields in Table 13.8 are typical for the kraft process which usually ranges from 40 to 55 %. Wood to pulp conversion factors are based on equivalent weights of woody material and so are similar between species (Kibblewhite, 1984). Of more importance is chip basic density and, fibre (tracheid) length which affect paper quality. In comparison

with *P. radiata*, fibre dimensions are very similar. However basic densities are lower for *C. lanceolata*, corresponding to *P. radiata* pulpwood (Kibblewhite, 1984). Moderate values of tension resistance and burst index were found by de Lelles *et al.* (1978), and Foelkel *et al.* (1978) reported that tear and fold strengths were good. Extractive content also affects the economics of pulping by increasing cooking chemical demand (Lavery, 1986); and with a considerably larger content than *P. radiata* (see section 4.2) pulping is likely to be more costly. Table 13.8 indicates that *C. lanceolata* would be suitable for kraft pulping, although low chip basic density and high extractive content would result in lower pulp quality and higher costs compared to *P. radiata* pulp.

5. SUMMARY

Overall, mechanical and physical wood properties of New Zealand grown *C. lanceolata* are numerically lower than those of native grown *C. lanceolata*. This is consistent with experience with some other exotic species. The main factor is a lower basic density resulting in reduced strength. Shrinkage however appears to be fairly constant. Within-tree variation of physical properties is consistent with other trees, although an examination of extractive content would be of further use.

In comparison with *Pinus radiata*, *C. lanceolata* wood is not as dense and correspondingly not as strong. In this respect it is similar to *Sequoia sempervirens* and slightly stronger than *Cryptomeria japonica*. Shrinkage is similar for all four species and there is little degrade under conventional kiln schedule or air drying. Drying rates are similar to *P. radiata*. It appears that due to its low basic density *C. lanceolata* would be unsuitable for heavy structural uses. However its dimensional stability, ease of drying and reputed durability would allow it to be used in weather-boarding, panelling, joinery *etc*..

Table 13.1: Height (Ht) and Diameter (D) Data For Stands of *C. lanceolata* (*Cryptomeria japonica* data are given in brackets)

Stand:		WF	LM	CH		EH
Ht (m)	Mean	12.2	14.3	23.1	(25.2)	23.5
	Max.	14.9	17.7	25.0	(26.6)	29.2
	Min.	10.8	10.3	20.5	(23.8)	18.1
	St. Dv.	1.41	2.6	1.96	(1.34)	
	n	10	12	15	(5)	5
D (cm)	Mean	19.9	28.9	39.0	(52.8)	67.5
	Max.	30.5	39.7	59.8	(86.7)	89.0
	Min.	13.0	20.2	18.9	(39.1)	51.0
	St. Dv.	3.26	5.8	8.62	(20.2)	
	n	30	12	100	(5)	5
Approx. Age (yrs)		25	25	58	58	57

Notes: WF: Whakarewarewa Forest. LM: Longmile, GTI. Rotorua
CH: Camp Huinga. New Plymouth. EH: Eastwood Hills Arboretum. Gisborne.

Table 13.2: Cumulative Volumes, Heartwood and Density of *C. lanceolata* Trees (LM, Longmile; CH, Camp Huinga)

Ht (m)	Volumes (m^3)			Densities (kg m^{-3})		MC(%)
	Total	Htwd.	Htwd %	Basic	Green	
LM 4						
1.3	0.067	0.029	43.7	335	1094	226
3.0	0.134	0.053	39.5	327	1093	235
6.0	0.216	0.073	33.8	313	1083	247
9.0	**0.271**	**0.095**	**34.9**	**309**	**1076**	**248**
LM 12						
1.3	0.073	0.018	24.7	326	1065	226
3.0	0.121	0.028	23.1	325	1051	223
6.0	0.171	0.033	19.0	321	1044	224
9.0	**0.200**	**0.033**	**16.6**	**320**	**1047**	**226**
CH 4						
3.0	0.476	0.300	63.1	295	810	175
6.0	0.752	0.472	62.8	287	754	163

9.0	**0.979**	**0.608**	**62.1**	**284**	**729**	**157**
12.0	1.164	0.712	61.2	284	721	154
15.0	1.307	0.783	59.9	286	721	152
18.0	1.412	0.826	58.5	287	725	153
21.0	1.474	0.848	57.5	288	729	153
CH 9						
3.0	0.228	0.111	48.9	324	915	182
6.0	0.333	0.164	49.3	317	873	175
9.0	**0.417**	**0.202**	**48.6**	**314**	**855**	**172**
12.0	0.482	0.227	47.1	315	850	170
15.0	0.529	0.243	45.9	317	851	168
18.0	0.558	0.250	44.7	317	851	168
CH 14						
3.0	0.311	0.189	60.9	317	978	209
6.0	0.482	0.268	55.6	314	948	202
9.0	**0.621**	**0.323**	**52.0**	**312**	**921**	**195**
12.0	0.730	0.369	50.6	310	905	192
15.0	0.812	0.406	50.0	310	896	189
18.0	0.869	0.428	49.2	310	892	188
21.0	0.903	0.435	48.2	310	893	188
CH 41						
3.0	0.163	0.087	53.3	355	968	173
6.0	0.261	0.142	54.3	349	925	165
9.0	**0.340**	**0.177**	**52.2**	**345**	**907**	**163**
12.0	0.401	0.200	49.9	344	899	161
15.0	0.438	0.209	47.8	343	898	162
CH 42						
3.0	0.346	0.163	47.1	345	1010	193
6.0	0.495	0.226	45.6	339	994	193
9.0	**0.617**	**0.274**	**44.3**	**337**	**973**	**189**
12.0	0.717	0.311	43.3	337	957	184
15.0	0.796	0.335	42.2	338	950	181
18.0	0.852	0.350	41.1	339	949	180

Whole tree means:

LM	0.234	0.064	27.4	315	1062	
CH	0.845	0.418	49.5	319	864	

Table 13.3: Non-cumulative (Weighted Mean) Densities, Moisture Content and Volumetric Shrinkage of *C. lanceolata* (LM, Longmile; CH, Camp Huinga)

Ht (m)	Green Density	Basic Densities (kg m^{-3}) Total	Htwd	Sap	MC(%)	Volumetric Shrinkage (%)
LM 4						
0.0	1088	334			226	
1.3	1102	338			226	
3.0	1081	292			271	
6.0	1045	290			260	
9.0	**1053**	**305**			**245**	
LM 12						
0.0	1078	326			231	
1.3	1041	328			217	
3.0	1009	314			221	
6.0	1054	313			236	
9.0	**1082**	**311**			**247**	
CH 4						
0.0	877	303	300	313	190	7.9
3.0	671	281	272	298	139	8.0
6.0	639	264	256	280	151	8.0
9.0	**656**	**284**	**283**	**283**	**131**	**8.6**
12.0	703	289	287	292	143	9.0
15.0	754	311	316	305	143	7.9
18.0	797	299	305	291	166	8.8
21.0	859	303	339	284	184	8.3
CH 9						
0.0	961	331	318	350	190	8.5
3.0	777	304	285	323	156	8.5
6.0	792	303	283	327	161	9.5
9.0	**773**	**303**	**292**	**313**	**155**	**9.0**
12.0	872	344	354	335	154	9.8
15.0	835	317	294	326	164	9.4
18.0	906	326	326	327	178	9.8
CH 14						
0.0	1013	322	321	328	215	11.4
3.0	898	306	300	312	193	10.2
6.0	864	311	309	312	178	10.2
9.0	**816**	**301**	**297**	**307**	**171**	**10.1**

12.0	813	303	312	295	169	9.8
15.0	811	305	310	299	166	9.3
18.0	882	315	329	309	180	9.4
21.0	998	334	361	327	199	9.1
CH 41						
0.0	1022	364	373	348	181	9.9
3.0	859	338	333	343	154	9.5
6.0	848	340	336	345	150	10.9
9.0	**851**	**328**	**329**	**329**	**159**	**10.8**
12.0	862	345	375	329	150	12.1
15.0	925	302	313	298	206	10.1
CH 42						
0.0	1017	351	350	350	190	8.9
3.0	988	327	315	340	203	8.8
6.0	918	326	327	326	181	10.0
9.0	**856**	**330**	**318**	**336**	**160**	**9.5**
12.0	854	341	329	349	150	9.4
15.0	929	356	350	360	161	9.9
18.0	940	356	359	355	164	9.5

Table 13.4: Dimensional and Volumetric Shrinkage of *C. lanceolata* at 3.0 m (green to oven dry)

Tree	Dimensional Shrinkage (%)			Volumetric Shrinkage (%)	
	Lon	Rad	Tan		(From Table 13.3)
CH 4	0.13	3.1	6.0	9.2	8.0
CH 9	-0.03	3.0	6.4	9.4	8.5
CH 14	-0.08	3.5	5.6	9.0	10.2
CH 41	0.10	3.2	6.2	9.5	9.5
CH 42	-0.06	3.0	5.6	8.5	8.8
Mean	**0.01**	**3.2**	**6.0**	**9.1**	**9.0**

Table 13.5: Drying Time (days) to Various Moisture Contents (%)

MC:	60%			30%			15%		
Schedule	n	mean	s.d.	n	mean	s.d	n	mean	s.d.
Kiln	24	2.5	2.6	24	5.5	2.4	13	7.0	2.5
Air	24	29.2	19.6						

Table 13.6: Mean Volumetric and Dimensional Shrinkages (%) After Drying (trt) and Following Recovery by Steaming (rec)

Schedule	Vol_{trt}	Rad_{trt}	Tan_{trt}	Vol_{rec}	Rad_{rec}	Tan_{rec}
Kiln	5.74	1.89	3.87	5.73	2.12	3.61
Air	3.53	1.06	2.75	5.38	1.82	3.60

Table 13.7: Mechanical Tests on *C. lanceolata* Small Clear Specimens

Test	n		Green	Air dry
Physical Properties	36	Basic Density (kg/m^3)	315	339
		Nominal Density (kg/m^3)	800	385
		Moisture Content (%)	154.2	13.6
Static Bending	36	MOE (GPa)	6.03	7.43
		MOR (MPa)	38.92	51.00
		FSPL (MPa)	24.57	32.51
Compression (Parallel)	36	MCS (MPa)	19.17	28.79
		CSPL (MPa)	17.01	21.06
Shear (Parallel)	72	MSS (MPa)	5.66	7.73

Table 13.8: Some Kraft Pulp, Chemical and Anatomical Properties of *C. lanceolata.*

Source:	1.	2.	3.	4.	5.
Pulp Yield (%)	45	37/43 *	46 - 52	-	-
Kappa Number	22-25	25/48 *	26 - 38	-	-
Fibre Length (mm)	-	1.94	2.51 - 3.41	3.01 - 3.35	2.02 - 4.55
Fibre Width (mm)	-	35.9	35 - 48	39 - 45	11.4 - 49.9
Specific Gravity	Low	0.33	0.31 - 0.40	0.38 - 0.49	-
Extractives (%)					
Alcohol/Benzene	3.4	3.88	-	5.6	-
Total	-	10.73	-	23.9	-

Notes: * Values refer to barked and unbarked wood respectively.

1. Foelkel *et al.*, 1978. 2. de Lelles *et al.*, 1978. 5. Lu, 1985.

3. Liu, 1982. Values represent range from six plantations.

4. Chang and Duh, 1988. Heartwood values only.

Table 13.9: Comparative Wood Properties of New Zealand, Chinese and Taiwanese Grown *C. lanceolata.*

	NZ	Taiwan [1]	China [2]	China [3]	China [4]
Densities (kg/m^3)					
Air Dry (12% mc)	385	-	310 - 346	-	296 - 435
Basic	339	310 - 400	358 - 411	295 - 423	-
Shrinkage, to 12% mc (%)					
Radial	1.8	1.5 - 1.9	-	-	0.8 - 1.3
Tangential	3.9	2.6 - 3.3	-	-	2.0 - 3.0
MOE (GPa)					
Air Dry	7.4	7.5 - 10.3	6.6 - 10.6	-	5.1 - 9.6
MCS (MPa)					
Air Dry	28.8	28.1 - 55.4	35.3 - 43.3	25.4 - 44.6	24.7 - 42.6

Notes: 1. Liu, 1982. Values represent range from six plantations.

2. Lin,*et al.*,1984. Values represent range from six plantations.

3. Yeh and Ch'en, 1964. Values represent range from three plantations, age 15 - 36 years.

4. Ko, 1958. Values represent range from sixteen plantations.

Table 13.10: Comparative Wood Properties of Four NZ Grown Exotic Species

	Cunninghamia lanceolata	*Pinus radiata*	*Sequoia sempervirens*	*Cryptomeria japonica*
Densities (kg/m^3)				
Air Dry (12% mc)	385	480	362	350
Basic	339	400	~330	300
Shrinkage, to 12% mc (%)				
Radial	1.8	1.9	2.2	2.1
Tangential	3.9	3.5	3.6	4.0
Volumetric	5.7	5.8	5.8	6.6
Shrinkage, oven dry (%)				
Longitudinal	0.01	0.11	0.04	
Radial	3.2	3.4	2.5	
Tangential	6.0	6.2	5.7	
Volumetric	9.0	9.8	8.4	
MOE (GPa)				
Green	6.0	5.5	6.4	
Air Dry	7.4	8.1	6.6	5.4
MOR (MPa)				
Green	39	38	56	
Air Dry	51	85	63	56
FSPL (MPa)				
Green	25	16		
Air Dry	33	41		
MCS (MPa)				
Green	19.2	15.4	23.6	
Air Dry	28.8	36.7	35.5	*30*
MSS (MPa)				
Green	5.7	5.2	5.7	
Air Dry	7.8	11.6	6.6	*5.0*

n.b. Numbers in italics refer to Japanese grown *Cryptomeria japonica.*

Figure 13.1: Overall Sawing Pattern and Mechanical Test Specimens

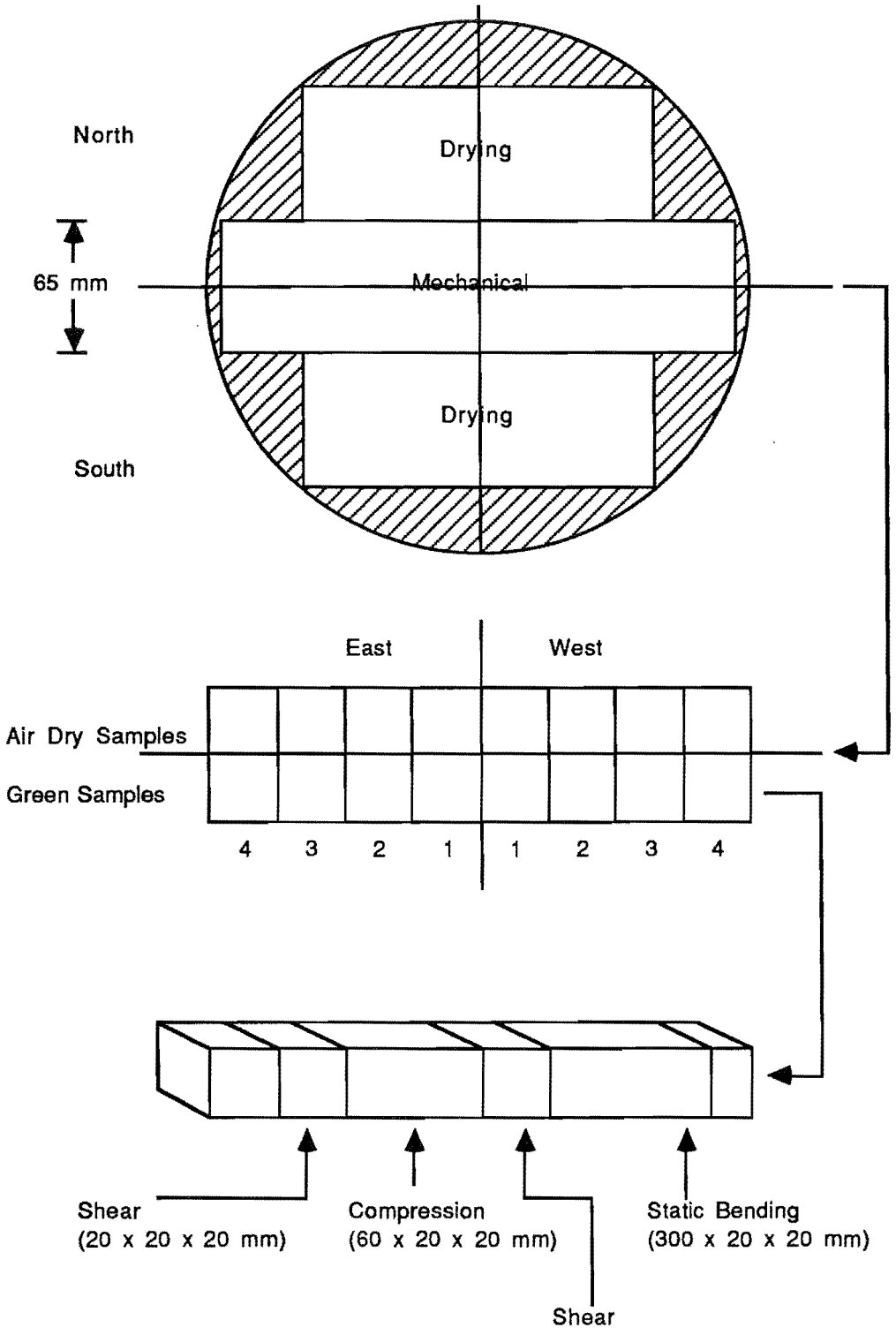
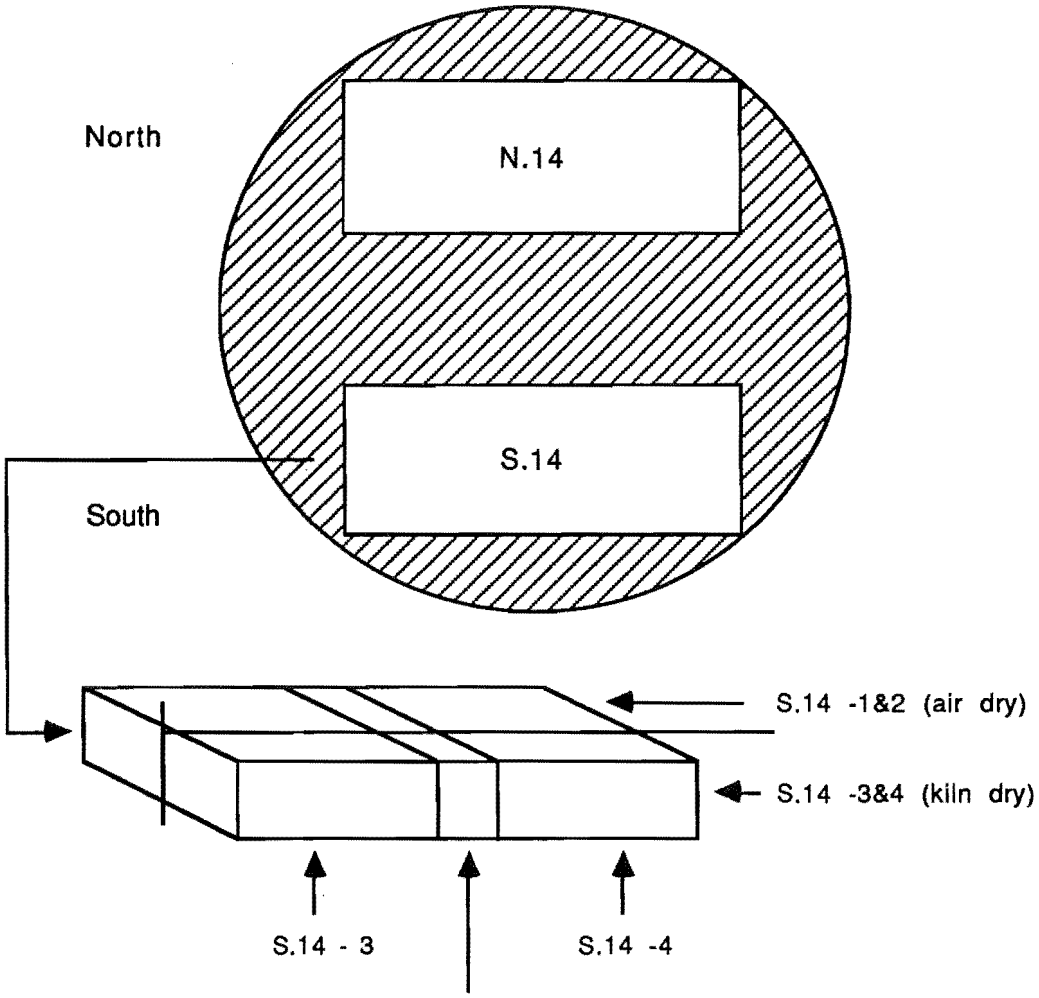
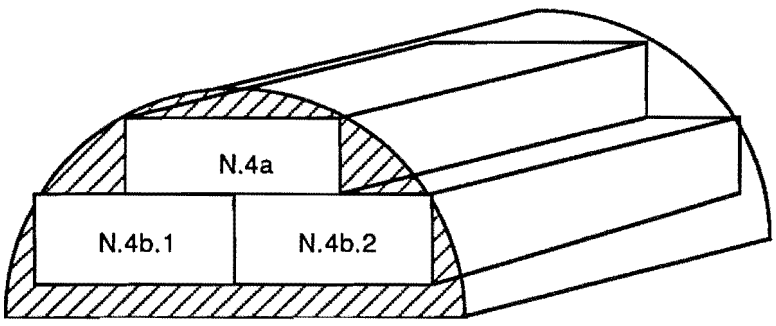


Figure 13.2: Drying Study Sawing Pattern





Drying Sample Labelling

Figure 13.3: Disc Weighted Mean Basic Densities

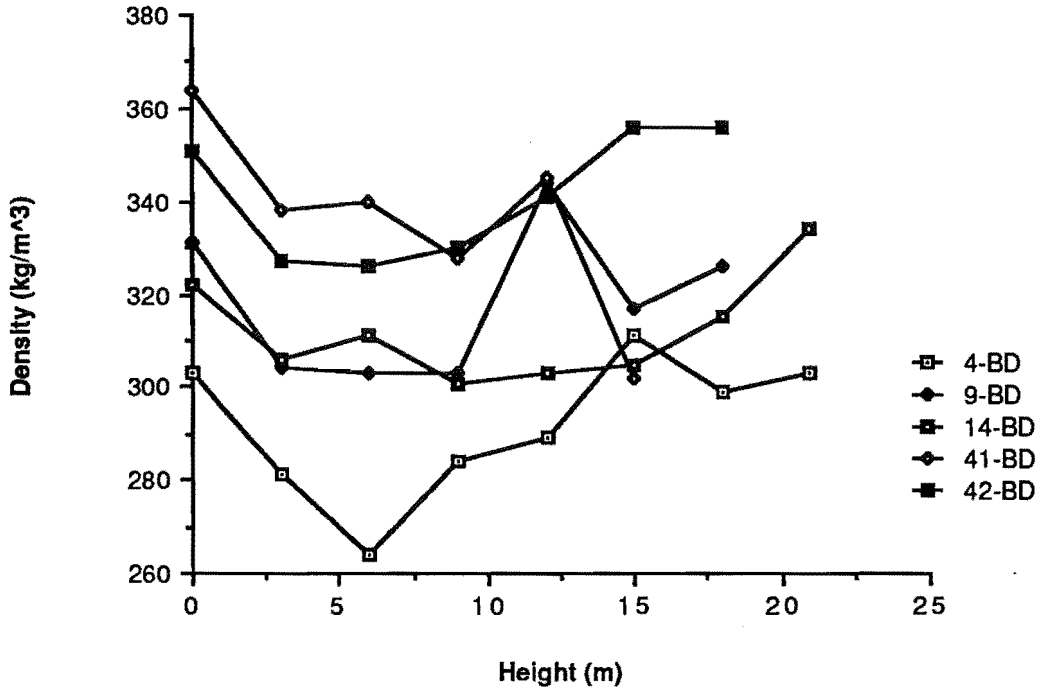


Figure 13.4: Disc Weighted Mean Moisture Contents

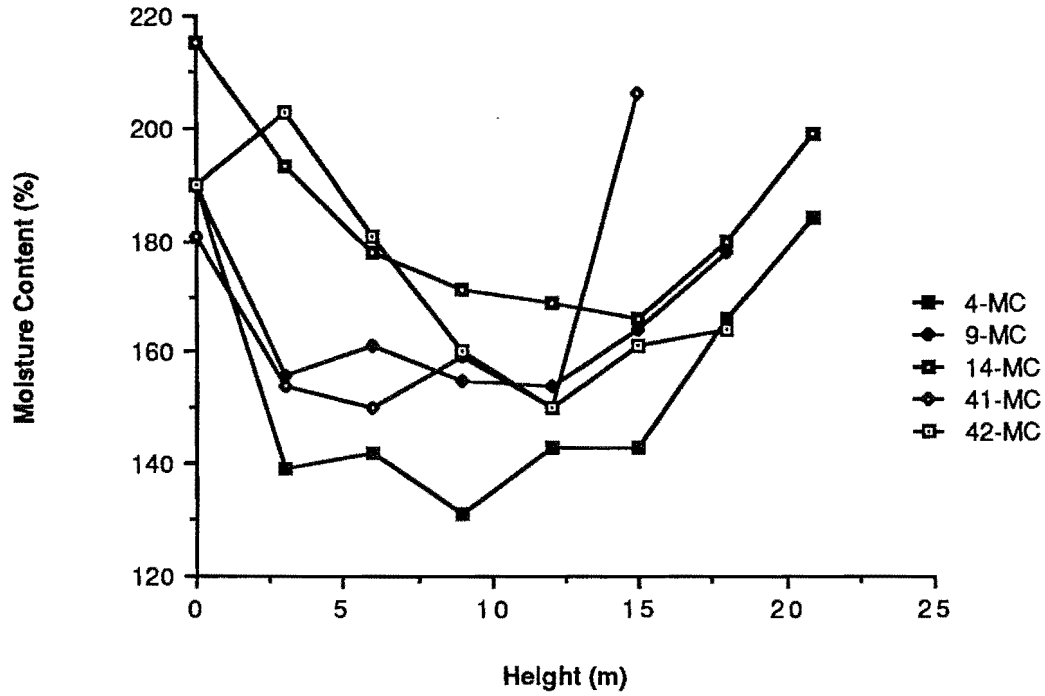


Figure 13.5: Disc Weighted Mean Basic Densities by Sites

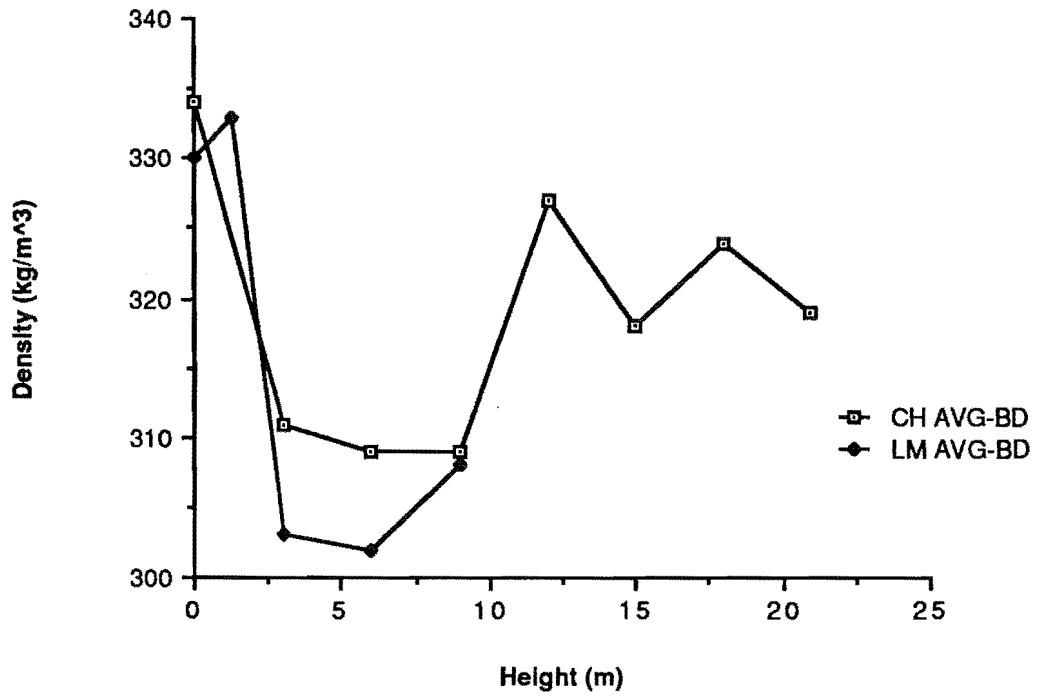


Figure 13.6: Basic Densities (5 Year Averages) From Core Samples

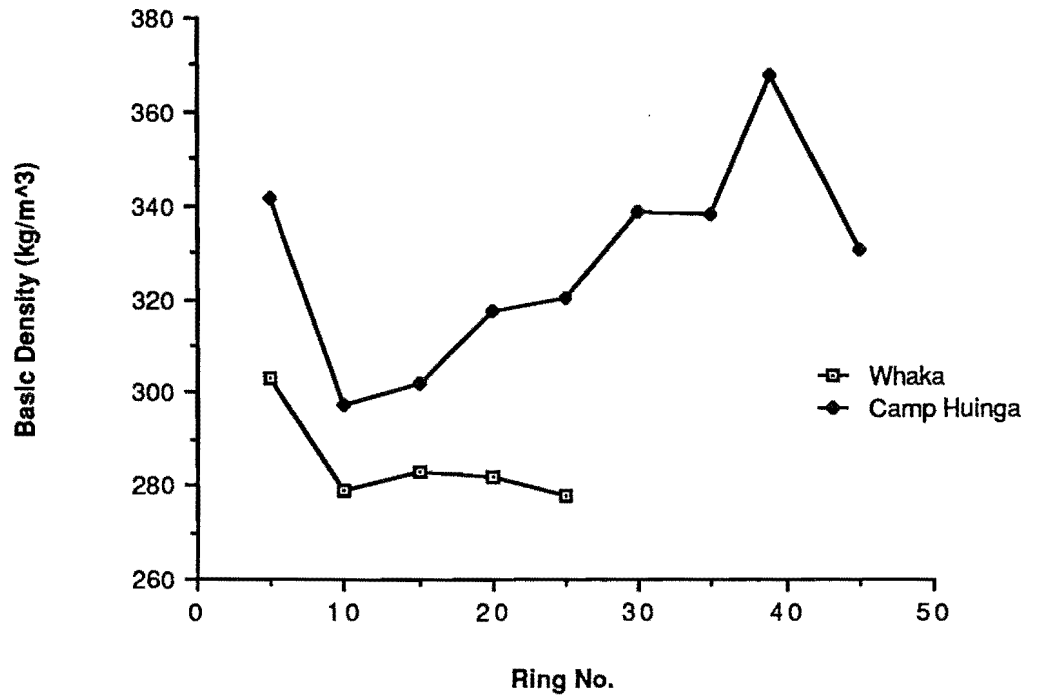


Figure 13.7: Drying Rates of *C. lanceolata* Samples

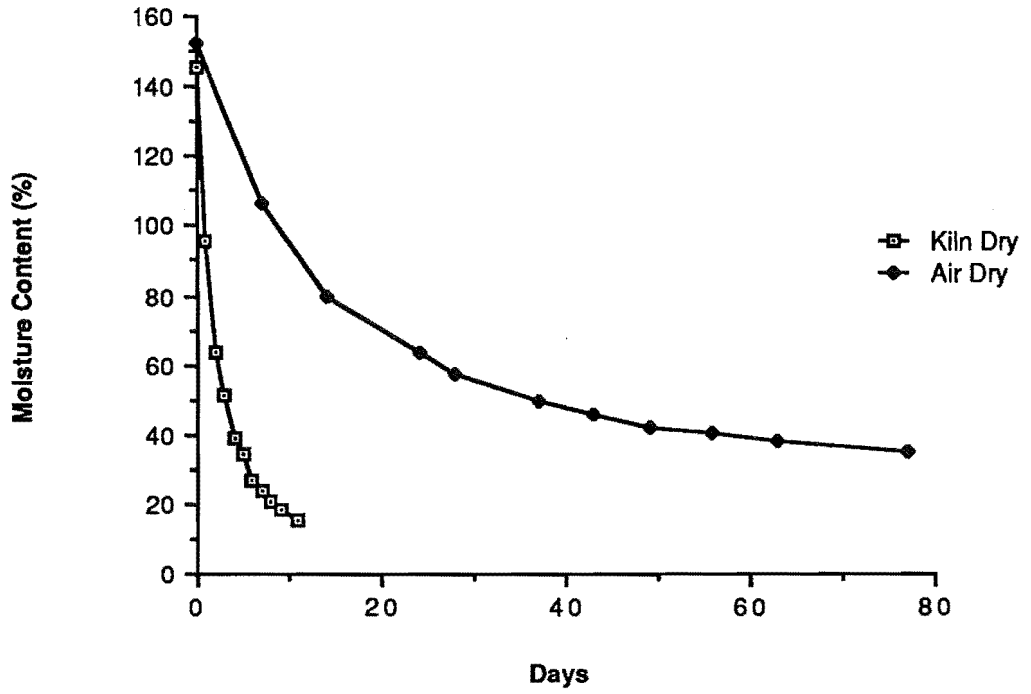


Figure 13.8: Drying Rates at Conventional Kiln Schedule

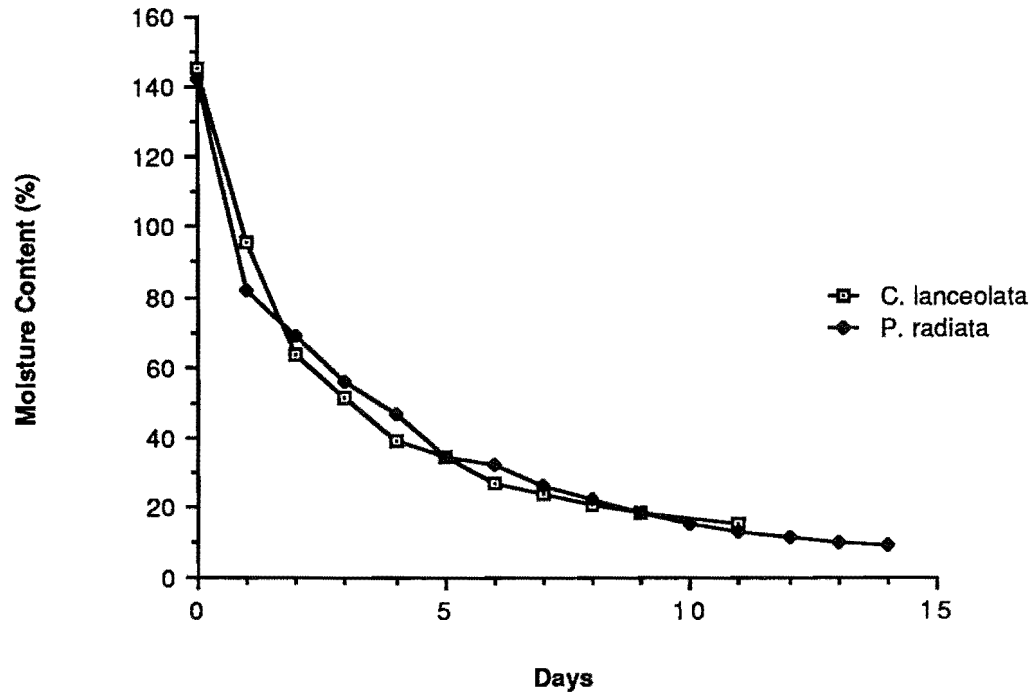
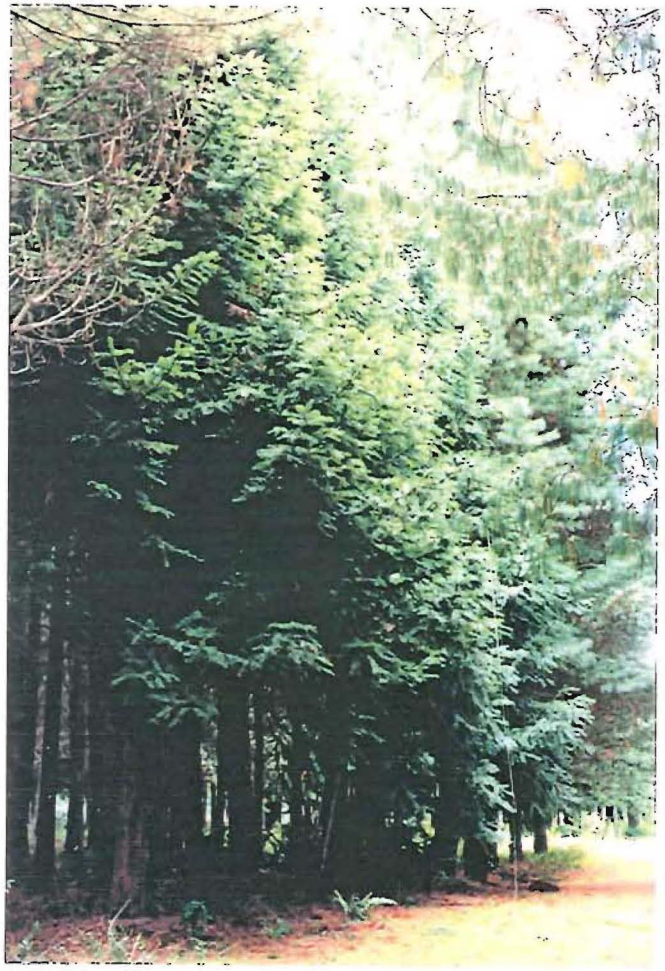


Plate 13.1: Stand of *C. lanceolata*, Camp Huinga

Plate 13.2: Plot of *C. lanceolata*, Longmile, GTI

(note 2 m pruning ladder against tree in the centre of the photo)



CHAPTER XIV

OPOSSUM PALATABILITY OF *Cunninghamia lanceolata* AND *Pinus radiata* SEEDLINGS

1. INTRODUCTION

Establishment of any new and untried tree species has a number of uncertainties. Even if abiotic factors such as silviculture and site requirements are known and can be met, biotic factors have to be considered; *e.g.* competition with other plant species, pathogens, insects and browsing animals.

C. lanceolata is a main timber species in central-southern China, where biotic limitations are not considered of significant importance (for a detailed review see chapter II). The species is apparently little used outside China and Taiwan, although it has been tested in a number of countries. Both climatic stress and animal browse have been cited as reasons for *C. lanceolata* 's failure to survive, at least in Queensland, Australia (R. Yule, Dept. For., Queensland, pers. comm.).

In New Zealand climatic site conditions appear to be, in some areas, suitable for the introduction of *C. lanceolata.* However the widespread distribution of opossums (*Trichosurus vulpecula*) throughout the country may be an important factor to consider. *P. radiata* is the most widely planted plantation species in this country and does not seem to be overly affected by damage from opossum browse. A comparison of the palatability of these two species to opossums would useful in predicting the success of establishment of *C. lanceolata* in opossum infested areas.

The aim of this experiment therefore is to observe and measure the palatability of *C. lanceolata* seedlings to opossums, in comparison to that of *P. radiata* seedlings.

2. MATERIALS AND METHODS

Two-year-old *C. lanceolata* and one-year-old *P. radiata* seedlings were used in the study; 24 seedlings of each species were used. The *C. lanceolata* seedlings were obtained from FRI, Rotorua nursery, grown from seed from Guizhou province, China. Seedlings were removed from the nursery beds in Rotorua and flown down to Christchurch on 17 May 1989 and replanted. Six weeks later 24 seedlings with "healthy" appearances were removed and taken to opossum pens at FRI, Rangiora. *P. radiata* seedlings were

obtained from the FRI, Rangiora nursery and removed as needed. Those seedlings were smaller in size but were a standard planting size for normal establishment of *P. radiata*.

Twenty two opossums were used in the experiment and were separated into two pens containing 9 (pen 1) and 13 (pen 2) animals. Pen 1 actually comprised three smaller pens linked by open doors at one end. All opossums had been taken from Ashley forest several months previously and had been kept in captivity since. While in captivity they had been fed a mixture of vegetables and fruit. By the time of the trial all opossums were settled and in a healthy condition.

Twelve seedlings of both species were allocated to each pen. In pen 1 four seedlings of each species were planted in a single row at 1 m spacings in each of the smaller pens. Within each row, species were randomly assigned positions. In pen 2 seedlings were planted at 1 m x 1 m spacings in 3 rows of 8 seedlings; species were randomly arranged. Seedlings were planted in mid-afternoon while the animals were resting. In addition, the usual food (a fruit and vegetable mixture) was placed at the feeding areas. The pen layouts are shown in Figures 14.1 and 14.2.

2.1 Measurements

Run 1 (27-28 June). Prior to the experiment, heights (in cm) of all seedlings were recorded. These were remeasured at 9.00 pm, 27 June and the next morning at 8.00 am, 28 June. Heights were then converted to percentages of original heights. Percentage of foliage remaining was also estimated the next morning.

In addition, categories of damage were recorded for each seedling by:

1. Position (tip, Ti; branch, Br; stem, St; none, No).
2. Amount of bark damage (severe, Se; moderate, Mo; light, Li).

Observations of feeding behaviour were made until 9.00 pm; this was in order to see if relative preferences existed between species.

Run 2 (28-29 July). On the following morning the damage done to the *C. lanceolata* seedlings was minimal (see results). It was therefore decided to repeat the experiment for the following night. Fresh *P. radiata* material was used and the old material discarded; the same *C. lanceolata* material from the first run was used as overall damage was slight. This run was an attempt to see if a second night of exposure to the new species (*C. lanceolata*) would result in any change of preference over the first night.

2.2 Analysis

As seedling layout was completely randomised each seedling was treated as an observation. Height and foliage measurements were analysed as follows (blocked by pens):

Source	degrees of freedom
Pen (PN)	1
Species (SP)	1
PN x SP	1
Error	44
TOTAL	47

For qualitative variables (browse position, bark damage) frequency distributions were compared between species using Chi-square tests.

3. RESULTS

3.1 Final Height and Foliage

Analysis showed highly significant differences between both species and pens ($p = 0.0001$). This was visually apparent both at measurement times in the evening and the following morning where the general case was that *P. radiata* seedlings were completely or almost completely stripped of all foliage and the stems had been completely chewed (Plates 14.1 and 14.2). In contrast *C. lanceolata* seedlings had little or no change in heights or foliage removed in the evening and only slightly more damage by the following morning. Table 14.1 shows height changes and foliage remaining.

Pen differences were as significant as species differences, with pen 2 showing consistently greater damage over pen 1. A number of factors are likely to cause this effect and are discussed later. The comparison between pens is (in a strictly statistical sense) not a valid comparison due to layout and opossum numbers; however in both cases the trend of greater damage to *P. radiata* over *C. lanceolata* is shown although the degree of difference is not the same.

As mentioned above, pen 1 was comprised of three smaller pens (Figure 14.1); analysing pen 1 separately by species and "sub pens" it appears that for *P. radiata* heights there was slight variation (but not significant at the 95 % level) of height damage between sub pens at the evening measurement, however this was not apparent by the morning

measurement. Foliage damage for *P. radiata* showed considerable differences between sub pens (Table 14.2).

3.2 Browse and Stem Damage

Use of Chi-square analysis meant that browse and stem damage was examined by species only. Analysis of species and pens showed no difference between pens for *P. radiata* and slight differences for *C. lanceolata* (pen 1 showing less damage then pen 2). As before, the trend of greater damage to *P. radiata* was evident in both pens although the magnitude of the differences between species was not the same in both pens.

Analysis of browse was carried out for each position separately and for browse at all combinations of positions. Highly significant differences were seen in all browse positions and stem damage. In all cases *P. radiata* seedlings had a greater frequency of damage than those of *C. lanceolata* ($p = 0.0006$ or 0.0001). Expected and observed values are shown in Tables 14.3 and 14.4.

3.3 General Observations

Feeding behaviour was generally consistent in that opossums appeared to browse initially on *P. radiata* seedlings and then *C. lanceolata.* In pen 2 there were three *C. lanceolata* seedlings that were heavily browsed (*i.e.* 60 %, 60 % and 20 % foliage remaining) and observation through the night indicated that these trees were browsed regularly (plates 14.3 and 14.4). All other *C. lanceolata* were not browsed in a sustained manner but were "nibbled" at occasionally; tips and branches were the most frequent browse position.

Pen 1 as mentioned showed less overall damage than pen 2. As shown in Table 14.2 most damage occurred in sub pen 3; in fact opossum numbers were mostly concentrated in this sub pen throughout the evening. Thus it would be logical to expect most damage to occur there.

3.4 Second Run

This was carried out the following night. Results were as for the first run and are given in Tables 14.5 - 14.7. Height and foliage percentages of *C. lanceolata* are based on initial measurements.

Highly significant differences for heights and foliage were again apparent between species ($p = 0.0006$ to 0.0001) and between pens ($p = 0.0001$). There was a marked reduction in foliage remaining on *C. lanceolata* seedlings in pen 2 suggesting that more browse was occurring than the previous night; however the pattern of complete stripping of *P. radiata* before browsing *C. lanceolata* was apparent.

The increase of damage to *C. lanceolata* can be seen in the increased number of seedlings being browsed in all browse categories and in increased numbers of severe and moderate bark damage. Again, however for the most part, damage was significantly less than that for *P. radiata.*

4. DISCUSSION

Results from this trial would seem to indicate that opossums have a very strong preference for *P. radiata* seedlings over *C. lanceolata* seedlings. However a number of factors should be considered before these results are applied to a field situation.

Although there was a clear preference for *P. radiata* seedlings it should be noted that the opossums, although settled in captivity, were taken from Ashley forest. Thus the opossums were already familiar with *P. radiata* as a food source and this could be expected to introduce a bias towards *P. radiata* in the trial. In order to reflect a true preference it would be necessary to use opossums that have not been exposed to either species previously and would therefore regard both species as new potential food with (initially) equal caution and/or curiosity.

Nevertheless the comparison is still valid in terms of a "normal" forestry situation where it would be reasonable to assume that plantings of a new species within an established forest would be in proximity to stands of *P. radiata.* The trial therefore may reflect this situation; the results indicating that *C. lanceolata* is, at least initially, not preferred to existing food resources.

Seedling age and condition are other factors which must be taken into account. One year old *P. radiata* was used (normal planting age) with a mean initial height of 33 cm, as opposed to two year old *C. lanceolata* with a mean height of 53 cm. The younger *P. radiata* may have been more palatable due to softer tissue or a higher concentration of sugars or other palatable substances. This could be caused either by differences in age and thus development (*e.g.* Kozlowski, 1971), or nursery condition. *P. radiata* seedlings were obtained direct from the nursery beds at Rangiora and so were under very little stress. Conversely the *C. lanceolata* stock had been root wrenched and undercut prior to lifting in Rotorua, then air freighted down to Canterbury and replanted twice. Foliage turned to a distinctive red-brown colouration in response to this treatment; translocation of sugars/carbohydrates would be expected to take place in response to root injury conditioning (Duryea, 1984) so that by the time of the experiment a considerable change in foliar composition may have occurred.

While the observed response was similar in both pens (*i.e.* marked preference for *P. radiata*) there was a significant difference between pens. Differing numbers of opossums

and layout are most likely to have caused the difference. The layout of pen 1 (using three "sub pens") was adopted to give a similar overall size to that of pen 2, however access between sub pens was only by doors at the feeding end of the pen and was thus substantially reduced. Coupled with this was the observation that the opossums in this pen appeared to stay mostly in sub pen 3, occasionally in sub pen 2 and very rarely ventured into sub pen 1. Consequently overall damage was not as marked as in pen 2 although damage within sub pens increased with increased opossum numbers; this is seen in Table 14.2.

Long term exposure of opossums to *C. lanceolata* may give a different response to that obtained in this experiment. It is somewhat surprising that such a marked preference should be exhibited for *P. radiata*; in China and Taiwan *C. lanceolata* is browsed by squirrels (Wu and Tai, 1982) and appear to be preferred over most other conifers (Kuo *et al.*, 1984). Details are given in chapter II, section 3.1.

Similarly browsing pests (in conjunction with frost and drought) appeared to limit the prospects for *C. lanceolata* in Queensland where it has been tried experimentally (Nielson, Dept. For., Queensland, pers. comm.); pests were wallabies, opossums and rats indicating appeal to a broad range of browsing animals. Browsing of *C. lanceolata* was in preference to native vegetation such as Hoop pine (*Araucaria cunninghamii*), and was important at establishment and during early years (R. Yule, Dept. For., Queensland, pers. comm.).

Long term palatability of *C. lanceolata* is therefore still an important factor; and once the *P. radiata* stock had been exhausted (and not replaced) defoliation of *C. lanceolata* was complete after two nights (Morgan, FRI, Rangiora pers. comm.). It is likely then, that once opossums are familiar with *C. lanceolata* as a food source increased damage would result. A field trial in a forest situation may show if longer exposure to opossums results in increased browse.

Preference for one plant over another is due a number of factors (smell, morphology, seasonal composition, attractive/repulsive volatiles *etc.*) and can vary between individual opossums, and opossum concentrations (Edwards, 1978). Palatability appears to be strongly influenced by 'salicin' content among poplar clones (*Populus spp.*), those with high 'salicin' content being generally less preferred (Edwards, 1974 ; 1978). Similarly, between-tree resistance of *C. lanceolata* to bark biting from squirrels has been related to the presence or absence of a second allele of peroxidase (Huang *et al.*, 1982). Field trials have been carried out for other species (*Pinus spp.*, *Picea spp.*) and browsing animals such as voles, moose, roe deer and snowshoe hares (*e,g,* Hansson, 1985; Bergeron and Tardif, 1988). Variation in 'resistance to palatabilty' was also seen in one trial; Hansson (1985) found that certain provenances of *Pinus contorta* were more severely attacked by voles than others and related this to the provenances' growing season.

5. SUMMARY

Results of this trial show that opossums previously exposed to *P. radiata* show a marked preference (almost to exclusion) for *P. radiata* over *C. lanceolata* seedlings. This may reflect a forest situation where opossums are presented with a new (potential) food source (*C. lanceolata*) and indicates that opossum damage at establishment of *C. lanceolata* may, at least initially, not be a problem.

Field trials would better show the effect of prolonged exposure to opossums and thus give a long term situation in which *C. lanceolata* is not regarded as a 'novelty'. Once opossums become familiar with the species as a food source damage is likely to increase; indications from overseas experience suggest that browse damage could be significant.

Table 14.1: Run 1 (27-28/6) Remaining Heights (as % of Original) at Evening and Morning and Remaining Foliage (as % of Original) at Morning

Variable	Time	Species	Pen 1	Pen 2	Total
Height	9.00 pm	*P. radiata*	87.4	42.9	65.1
		C. lanceolata	100.0	89.3	94.7
	8.00 am	*P. radiata*	74.6	42.9	58.7
		C. lanceolata	97.6	86.2	91.9
Foliage	8.00 am	*P. radiata*	30.0	1.3	15.6
		C. lanceolata	97.9	82.1	90.0
		Pen Totals	64.0	41.7	52.8

Table 14.2: Run 1 (27-28/6), Pen 1 Remaining Heights (as % of Original) at Evening and Morning and Remaining Foliage (as % of Original) at Morning

Variable	Time	Species	Subpen 1	Subpen 2	Subpen 3	Total
Height	9.00 pm	*P. radiata*	100.0	83.8	78.4	87.4
		C. lanceolata	100.0	100.0	100.0	100.0
	8.00 am	*P. radiata*	79.2	68.7	75.9	74.6
		C. lanceolata	97.4	97.9	97.5	97.6
Foliage	8.00 am	*P. radiata*	60.0	22.5	7.5	30.0
		C. lanceolata	97.5	97.5	98.8	97.9
		Pen Totals	78.8	60.0	53.1	64.0

Table 14.3a: Observed and Expected Seedling Numbers of Separate Browse Categories

	P. radiata	(Expected)	*C. lanceolata*	Totals
Ti*	24	(18.5)	13	37
No*	0	(5.5)	11	11
Br*	23	(14.5)	6	29
No	1	(9.5)	18	19
St*	21	(12.0)	3	24
No	3	(12.0)	21	24

* See section 2.1 for definition of symbols

Table 14.3b: Run 1 (27-28/6) Observed and Expected Seedling Numbers of Grouped Browse Categories

Damage	*P. radiata*	(Expected)	*C. lanceolata*	Totals
Ti Br St	21	(12.0)	3	24
Ti Br	2	(2.5)	3	5
Ti	1	(4.0)	7	8
No	0	(5.5)	11	11

Table 14.4: Run 1 (27-28/6) Observed and Expected Seedling Numbers of Stem Damage

Damage	*P. radiata*	(Expected)	*C. lanceolata*	Totals
Se*	17	(10.5)	4	21
Mo*	4	(12.0)	20	24
Li*	3	(1.5)	0	3

* See section 2.1 for definition of symbols

Table 14.5: Run 2 (28-29/6) Remaining Heights (as % of Original) at Evening and Morning and Remaining Foliage (as % of Original) at Morning

Variable	Time	Species	Pen 1	Pen 2	Total
Height	9.00 pm	*P. radiata*	81.5	72.6	77.1
		C. lanceolata	93.7	80.2	87.0
	8.00 am	*P. radiata*	75.5	55.7	65.6
		C. lanceolata	87.8	70.0	78.9
Foliage	8.00 am	*P. radiata*	17.5	0.0	8.8
		C. lanceolata	87.5	35.0	61.2
		Pen Totals	52.5	17.5	35.0

Table 14.6a: Run 2 (28-29/6) Observed and Expected Seedling Numbers of Separate Browse Categories

Browse	*P. radiata*	(Expected)	*C. lanceolata*	Totals
Ti	24	(23)	22	46*
No	0	(1)	2	2
Br	23	(19)	15	38
No	1	(5)	9	10
St	22	(17)	12	34
No	2	(7)	12	14

* Not significant at 95%

Table 14.6b: Run 2 (28-29/6) Observed and Expected Seedling Numbers of Grouped Browse Categories

Browse	*P. radiata*	(Expected)	*C. lanceolata*	Totals
Ti Br St	22	(17)	12	34
Ti Br	2	(2)	2	4
Ti	0	(4)	8	8
No	0	(1)	2	2

Table 14.7: Run 2 (28-29/6) Observed and Expected Seedling Numbers of Stem Damage

Damage	*P. radiata*	(Expected)	*C. lanceolata*	Totals
Se	19	(13.5)	8	27
Mo	3	(3.0)	3	6
Li	2	(7.5)	13	15

Figure 14.1: Pen 1 Layout

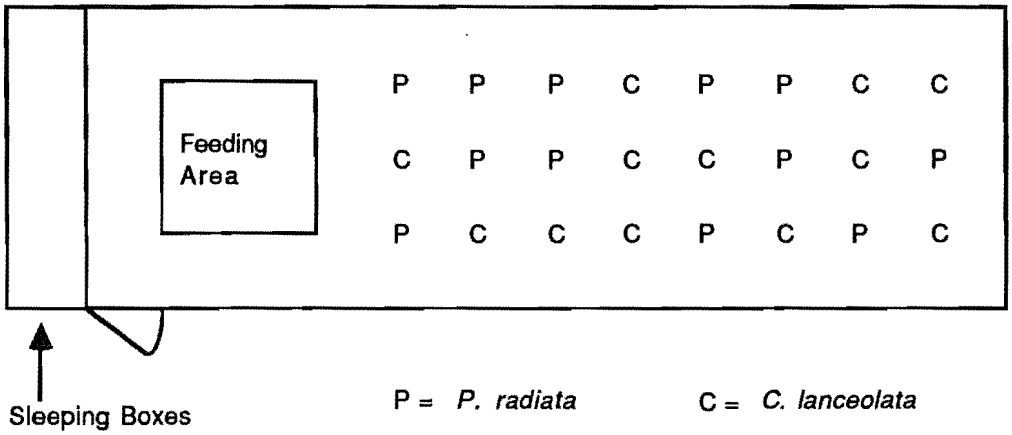


Figure 14.2: Pen 2 Layout

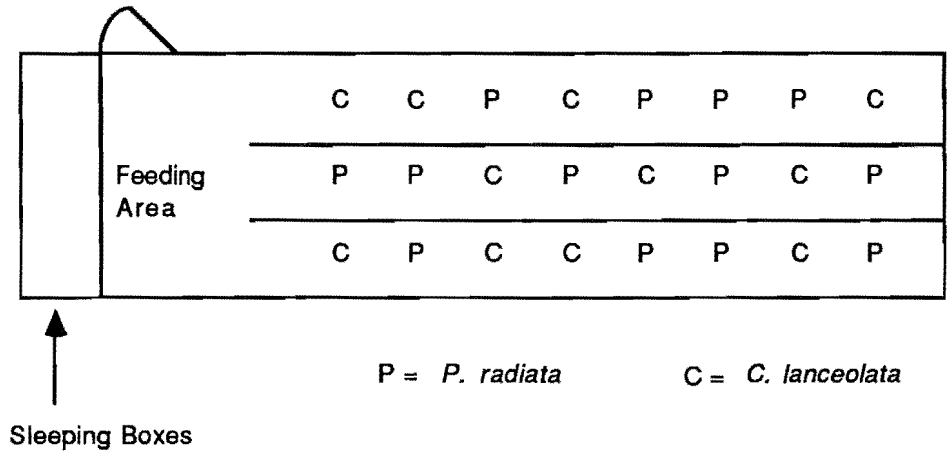


Plate 14.1: *P. radiata*, Before First Run

Plate 14.2: *P. radiata*, After First Run

Plate 14.3: *C. lanceolata*, Before First Run

Plate 14.4: Severe Damage of *C. lanceolata*, After First Run

CHAPTER XV

CLIMATE MODELLING

1. INTRODUCTION

While *C. lanceolata* has been extensively used in China for many centuries its planting as an exotic species has been quite limited. In considering the performance of *C. lanceolata* in New Zealand this study has concentrated on characterising the environmental conditions in its native country and those most conducive to its growth (by way of physiological experiments). A brief examination of its experience as an exotic and its performance in new environments is also necessary, as this can provide further information with respect to what factors limit growth in these new environments and what conditions the species can tolerate outside of its natural range.

The use of climate modelling for species suitability is also reviewed. Climate is a major determinant of vegetation distribution on a regional scale, and the daily and seasonal fluctuations of available heat and water are the most critical factors in plant distribution (Spurr and Barnes, 1980). Climate modelling can be useful in determining a broad picture of species suitability to particular areas; it is therefore applicable to this study in order to identify areas in New Zealand that possibly could be suitable for *C. lanceolata.* Two climate models are used to illustrate this. The first is WORLD, a global scale model developed by Dr Trevor Booth (CSIRO); at the time of use the WORLD model had just been released and is thus still in the early stages of development. The second climate model is more detailed and concerned specifically with New Zealand, it has been developed by Dr Neil Mitchell (University of Auckland); using similar techniques to the WORLD model.

2. EXOTIC PLANTINGS

2.1 Trials and Plantations

Outside of China *C. lanceolata* has been tried experimentally in a number of countries; Japan, South Africa, Argentina, Australia, France, and Malaysia. There is only one other country, Brazil, where it is grown commercially albeit on a small scale. As mentioned in chapter XIII, New Zealand has two sites where *C. lanceolata* has been planted for non-

ornamental use (New Plymouth and Rotorua). As an ornamental species, trees have been planted in botanical gardens and parks throughout the country, usually in pairs or singly.

The species is widely planted in Britain and Europe (Streets, 1962; Dallimore and Jackson, 1931; Den Ouden and Boom, 1982) although mainly as an ornamental. There is also reference to its cultivation in the eastern United States, presumably as an ornamental (Welch, 1991), and it is noted in Wright (1962) as having greater potential importance in the northeast United States than the native species. As yet there is no mention in the literature of the species having been trialed in these places. It is not considered to be frost hardy, being susceptible in particular to early frosts (Den Ouden and Boom, 1982). Some experimental work has been carried out in France; the species has been trialed for short rotation coppice (France, Association Forêt-Cellulose, 1982) and *in vitro* vegetative propagation, although specimens, it seems, were obtained from arboreta and not from larger scale plantings or trials (Bigot and Engelmann, 1987). There is also record of *Cunninghamia* being biologically successful and deserving of attention in France from its cultivation in the Arboretum des Barres (Wright, 1962). It does however appear that there is some variation in frost resistance in 50+ year old trees growing in France (Bigot and Engelmann, 1987). Webb *et al.* (1984) cite France, Netherlands, India and Brazil as seed sources. The extent of the plantings in the first three countries is not known.

Streets (1962) mentions its growth in Malaya (Malaysia) as moderate in open sites with good survival in Imperata grassland; seeds were obtained from trees in Hong Kong in 1952. Reference to Malaysia has also been made by Bigot and Engelmann (1987), although no recent data or plantings have been reported in the literature. There is similarly no references in the (English) literature to its use in other parts of Asia. However *C. lanceolata* has been trialed in Japan at the Tokyo University Forest in Chiba since 1958 (Negisi, pers. comm.). Elsewhere in Japan it is found as an ornamental, but again it appears that climate is limiting.

The species has become naturalised on the Black Sea coast of Adzhania (Caucasia) but regeneration usually fails (Mandzavidze and Matinjan, 1964). It has also been considered promising for Azerbayan (Afanas'ev, 1959) but it is not known if trials have been carried out. Richardson (1966) reported that *C. lanceolata* had been established in Asiatic Russia as a plantation species. He also suggested that it would do well in many Mediterranean countries, subtropical, and tropical regions of the world.

In Australia there have been a number of experimental trials in Queensland with a total area of 2.8 ha as at 31 March 1988 (Neilson, pers. comm.). The oldest trials were established in 1954 and the latitudinal distribution of all trials was between 17 ^{o} 20 'S to 28 ^{o}S. Early survival was good and form was considered good compared to *Araucaria cunninghamii* in some plots, but height growth was severely reduced by browsing. The species has not been successful due to a combination of factors including grass

competition, drought, waterlogged sites, and browsing (from rat, wallaby and possum); however there was some frost tolerance. Seed sources were from Brazil and Taiwan; while these are not considered as good provenances (see chapter III) it is unlikely that provenance selection would overcome the above factors.

There are documented reports of trials in South Africa. A 33 year old stand planted in 1922 had good growth (Streets, 1962); however the species has not been widely planted. A more recent trial was undertaken in 1983 using seed from three Taiwan provenances; the trial was in the Southern Cape Forest Region. Growth was poor after three years and *C. lanceolata* was considered unsuitable for commercial use (Zwolinski, 1988). No climate details were given so it is difficult to determine what factors contributed to the poor growth.

While there is only one reference in the English literature to *C. lanceolata*'s use in Argentina, the species has been trialed and initially appears promising (Golfari, pers. comm.). Results from a species trials in Puerto Piray, Misiones considered further trials of *C. lanceolata* to be worthwhile (Celulosa Argentina, 1958; Golfari and Barrett, 1967). Argentinian literature recommended it in the Sierras Grandes of Córdoba (Mármol, 1966), and it has been trialed in Tucumán (Niepagen, 1962). Work on frost resistance has been carried out in Misiones (Golfari,1962).

In neighbouring Brazil *C. lanceolata* has been extensively trialed and is used in commercial plantations (Golfari, 1968; 1970; 1975; Golfari *et al.*, 1978). Mensuration studies have been carried out (Heinsdijk and Soares,1962) and volume and yield tables have been constructed (Veillon and Silva, 1972). Here it is only grown in areas with little or no water deficiency. Growth and form are very good at Fazenda Levantina (Minas Gerais State; *ca.* 23 °S, 46 °W), and Caieiras (São Paulo State; *ca.* 23 ° 30 'S, 46 ° 40 'W). Initial growth was considered good on a variety of soils, including poor sandy soils (Guimarães, 1958). Although growth is good, site and climate limitations mean that plantings are on a small scale: 3900 hectares as at 1977 (Golfari *et al.*, 1978). Most of the plantings are carried out by one company, Companhia Melhoramentos de São Paulo - Industrias de Papel. There is also mention of *C. lanceolata* being used (experimentally) as an understory species to *Araucaria angustifolia* in São Paulo (Guidoni and Konecsni, 1982).

Trials further south in the states of Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS) have also shown good results, particularly at Blumenau-SC (*ca.* 27 °S, 49 °W) and Ibirana-SC. Other promising sites are at Curitaba-PR (*ca.* 25 ° 30 'S, 50 ° 40 'W) and Monte Alegre-PR (*ca.* 24 °S, 51 ° 30 ' W). As with the northern States of Minas Gerais and São Paulo, growth is good in many other sites but climate is often limiting. *C. lanceolata* was considered unsuitable at Jaboticabal in southern Brazil (Fonesca *et al.*,

1974). Golfari (1970) noted that *C. lanceolata* is sensitive to frost if planted in areas with uniform precipitation as this promotes continuous growth.

Sample height data, where available have been given in chapter II, Table 2.2.

2.2 Limitations to Species' Siting

For the purposes of this discussion, factors limiting siting are grouped according to climate (large scale abiotic), site conditions (small scale abiotic), and biotic (pests and diseases). It is too simplistic to attribute limitations solely to any one factor or group of factors, in reality it is usually interactions between factors that are important.

Temperature, for example, can be limiting at high levels due to protein denaturisation and thus disruption of enzyme systems. However, if plants are not adapted to high temperatures it is also likely that high temperatures are conducive to a build up of pathogen load, and this in turn restricts where the species can grow successfully. Similarly, low rainfall may not necessarily limit siting, depending on amount of rainfall in the growing season and length of water deficit (which in turn is related to temperature).

Climate contains the most limiting group of factors, in particular temperature and rainfall. As noted above there is often a complex interaction between factors. At its northern-most distribution in China, temperature is most likely to be limiting due to colder winter temperatures and reduced growing seasons; a description of climatic requirements has been given in chapter III. Cold (freezing) resistance varies between provenances but probably does not go much below -16 ^{o}C (see chapter VIII). Thus frost damage would occur more frequently and with more severity at the northern limits; and a reduced growing season may mean that recovery from frost injury is negligible. In Japan, colder temperatures are the most likely cause for limiting growth. This is evident from fossil remains of *C. lanceolata* in Japan up to the end of the Tertiary period. However subsequent cooling eliminated the species from the Japan islands (see chapter VIII).

Frost damage appears to be a major limiting factor in its use as an exotic in Europe and Latin America (Den Ouden and Boom, 1982; Golfari, 1963; 1970). Damage from early frosts in Britain, that occur during the active growing season, demonstrate the lack of adaptation to a variable climate (in terms of temperature). In China the seasonal climate is relatively stable from year to year and frosts are very rare in the growing season. This lack of adaptation is likely to be a problem in areas where climate is more variable (such as New Zealand) and has been shown to effect in the nursery trial where autumn frosts severely damaged seedlings that had not yet formed overwintering buds (chapter IV). Frost damage in Latin American countries (Brazil, Argentina) occurs through an interaction with rainfall pattern. In China the winter rest period of *C. lanceolata* is associated with cold and dry conditions. Golfari (1970) contends that planting in areas

that have uniform rainfall without water deficits, promotes continuous growth, which in turn makes *C. lanceolata* susceptible to frosts when normally it would have some resistance.

Amount of rainfall can also limit growth, drought is considered more limiting than frost in China within *C. lanceolata* 's geographic distribution (Hunan, FRI, pers. comm.). In China mean annual rainfall varies between 800 - 2000 mm in areas where *C. lanceolata* is planted and above 1200 mm in high yield areas. However in almost all areas of cultivation the rainfall pattern is heaviest during spring-summer months, corresponding to the active growing season. Where rainfall distribution is not "synchronised" with the growing period (*e.g.* either uniform or winter patterns) the lower rainfall limit would be expected to be somewhat greater in order to minimise water deficits. Many areas in Brazil were considered unsuitable for *C. lanceolata* due to water deficits (Golfari, 1968). In Queensland where drought was also considered more limiting than frost, mean annual rainfall was between 800 - 1234 mm (Neilson, pers. comm.). This probably reflects either unfavourable rainfall patterns and/or higher temperatures producing greater water loss.

Site factors also influence the growth and survival although to a lesser scale (*i.e.* unless climatic requirements are met plant growth will not occur even under ideal site conditions). Usually site factors are important in influencing growth rate rather than survival, but under extreme cases of unfavourable site selection (*e.g.* waterlogging, shade competition) survival may be at issue. General site conditions conducive for good growth for *C. lanceolata* include steep sloping ground, fertile, free draining soil, and shade.

In Queensland planting on flat sites prone to waterlogging resulted in poor survival (20 % after 16 years); form of the surviving trees was considered good, but growth was less than adjoining *Araucaria cunninghamii*. The requirement for well drained soils is also recognised in Brazil and the best plantations are located on steep sloped ground (Golfari, 1968; 1970). Similarly *C. lanceolata*'s soil fertility requirements are considered to be greater than many *Pinus spp.* indicating a high nutrient demand. Conversely it is considered less demanding (as to soil fertility) than *Cryptomeria japonica* and the native (Brazilian) *Araucaria angustifolia*, plantings are therefore also sited with respect to soil fertility.

Biotic limitations are not considered to be of economic significance in China, although biotic factors do affect growth to some degree (for a full review of pests and diseases see chapter II). This is most likely due to co-evolution with pests and diseases so that a degree of resistance has developed. When a species is placed outside its natural environment biotic factors may become important, either by the species not having

evolved any resistance, or from unfavourable climate or site factors that place the species under stress, thus increasing susceptibility to attack (Spurr and Barnes, 1980).

There have been no reported cases of insect damage limiting growth in the above countries where *C. lanceolata* has been used in trials or plantings. Because *C. lanceolata* is in a small genus (two species) it is considered to be comparatively pest free when used as an exotic (Wright, 1962). However in Queensland it has been noted that root rot was an important contributing factor to poor performance in at least one trial (Neilson, pers. comm.). This is possibly due to site factors; conversely in Tokyo *C. lanceolata* was resistant to white root rot (caused by *Rosellinia necatrix*) following serious outbreaks from 1976 - 1979; shade tolerance of *C. lanceolata* was thought to account for its resistance (Ito and Nakamura, 1984). On the other hand, root rot (*Pythium ultimum*) has been recorded in Sichuan (Qiu *et al.*, 1986).

Animal browsing in Queensland, principally by wallaby, but also by rat and opossum, was on a widespread scale and was considered a major limiting factor. Similarly in New Zealand there is definite susceptibility to possum browsing at the seedling stage, although less so than *P. radiata* (see chapter XIV). It seems that animal browsing then, is the most serious biotic limitation.

3. CLIMATE MODELS

3.1 Climate Classification

Climate classification has been attempted by a number of people for many years. Early work dates as far back as the mid nineteenth century (Thornthwaite and Hare, 1955), and while many classifications have been used none fully accounts for vegetation distribution. Köppen's climatic provinces, for instance, are broadly related to major vegetation types but have little correlation with actual distribution of vegetation in a specific area (Thornthwaite and Hare, 1955; Spurr and Barnes, 1980). Other systems such as Holdridge's life zones and Thornthwaite's system attempt a more realistic classification, accounting for interactions between climate variables, and have been used extensively in older exotic programs *e.g.* Brazil, South Africa (Booth, 1985). While attempting to classify climate into zones Thornthwaite and Hare (1955) acknowledged that climates themselves are continuous and therefore are inherently more difficult to classify. This depends greatly upon the accuracy of identifying climatic regions and their boundaries, and the correct parameters used to define these boundaries.

More recently the advent of readily available computers with the ability to store and process large amounts of data has made it possible to develop programs which more accurately map the seasonal fluctuations of climate on both a global and regional scale. In

using a database the need to zone climate is less important and a bioclimatic approach which is species specific can be taken. While the approach is not dissimilar to that as used in Brazil with the Thornthwaite system (*i.e.* matching similar climates), this is a more logical method as it deals directly and more accurately with a species' climatic requirements.

3.2 Computer Models

Work carried out by Nix, Busby and Hutchinson on the Bioclimatic Prediction System was further extended to the area of species suitability (identifying homoclimes for the introduction of a species within and between countries) by Booth (1985). Species suitability assessment was carried out in four stages:

1. Geocoding of distribution. Recording of specific locations representing the range of climatic environments where the species occurs.
2. Estimation of climatic data at locations.
3. Estimation of the species' climatic profile.
4. Identifying homoclime sites within the desired area of introduction.

Stages 2 and 3 were estimated using the BIOCLIM program which uses a climatic database and interpolates between points to construct surfaces for each climate variable. A climatic profile consisted of maximum and minimum values of 12 variables. Stage 4 was carried out by comparing this profile with meteorological stations in the area of introduction. If a location satisfied all 12 parameters it was given a suitability rating of 1 (similar climate to those in stage 1); a rating of 2 was given if locations satisfied four key parameters (mean annual temperature, minimum temperature of coldest month, mean annual precipitation, precipitation of the driest quarter); if locations failed on these four parameters they were considered unlikely to be suitable for the species.

How reliable this approach is depends on the accuracy of the climate data in both the original (source) area and the new intended area. Another consideration is that the extent of the species distribution may not entirely reflect the adaptability of the species; *i.e.* a species "realised niche," limited by ecological and historical factors, may be much smaller than its "fundamental niche" which is limited by physiological factors (Booth, 1985; Booth *et al.*, 1988). This is particularly so when dealing with the species' natural distribution, *e.g. P. radiata.*

The Bioclimatic Prediction System (BPS) has been widely tested for many Australian *Eucalyptus spp.* (Booth, 1985; Booth *et al.*, 1988) and some *Acacia spp.* (Booth, 1988a; Booth and Jovanovic, 1988). BPS identified many areas in Africa that were considered similar to climates in the natural distribution of *Eucalyptus citriodora* and compared these with actual trials in Africa (Booth, 1985). Sites which had ratings of 1 or 2 were

consistent with successful trials in or near those areas. There were cases where successful trials were not predicted by BPS, as their climates fell outside the source area; thus further modification of the climatic profile was needed to account for these sites. *Acacia holosericea* has also been analysed for Africa and the one known successful trial was predicted (Booth, 1988a). *A. mearnsii* climatic profiles based on natural sites in Australia, plantations in South Africa, and plantations world wide were compiled by Booth and Jovanic (1988); these were used to identify sites in China (Booth, 1988b). Results indicated a wide range of suitable sites (ratings of 1 or 2), but existing (successful) trial sites were identified only when world wide profiles were used.

These cases demonstrated the limits of the model if only natural sites are used for climatic profiles. However once new sites are known these can easily be incorporated and new profiles can be made. Further developments have lead to more detailed models for specific regions and countries; as more climate stations are included more accurate interpolation surfaces can be derived. The WORLD model described below has surfaces for Australia and Africa and climate stations for most other parts of the world. A similar model for China has been developed but uses different climate parameters (Booth and Hong, 1991), and a similar approach has been used for Korea (Noh, 1988). Dr Neil Mitchell at the Department of Botany, University of Auckland has also developed interpolated climate surfaces for New Zealand; these surfaces will be used to indicate what areas, if any, in New Zealand are suitable for *C. lanceolata.*

4. WORLD MODEL

The WORLD model, developed by Dr Trevor Booth, is a refinement of the BPS developed by Nix, Busby and Hutchinson. In this model six climate parameters only are used:

i) Mean annual rainfall (mm).
ii) Rainfall regime (summer/winter/uniform).
iii) Length of dry season temperature (months).
iv) Mean maximum temperature of the hottest month (^{o}C).
v) Mean minimum temperature of the coldest month (^{o}C).
vi) Mean annual temperature (^{o}C).

A full description is given in Booth *et al.* (1989) and Booth (1990). A data base of 15 391 locations is used and includes interpolated surfaces for Africa and Australia (Booth 1990). The species' climatic profile is manually entered into the program and the results displayed in map form showing suitable and unsuitable areas. Again, this program has been tested using mainly *Eucalyptus spp.* (Booth *et al.*, 1989; Booth, 1990; Booth and Pryor, 1991).

4.1 Climate Profiles of *Cunninghamia lanceolata*

The species so far tested by Booth and others have been almost all native to Australia and thus initial profiles have been compiled through extensive databases. In the case of *C. lanceolata* there is no such database; general climate descriptions are given by various authors in chapter III, there is also a list of climate parameters in Webb *et al.* (1984). Five climatic profiles were compiled from various sources:

1. Entire range in China. Webb *et al.* (1984).
2. Entire range in China. Watts (1969), Wu (1984).
3. Good sites in China. Cooperation Group of Chinese Fir, 1981b.
4. Best sites in China. Cooperation Group of Chinese Fir, 1981b.
5. Modified range (including two NZ sites), summer rainfall.
6. Modified range (including two NZ sites), winter and uniform rainfall.

The specifications are given in Table 15.1.

4.2 Distribution Patterns

A description of distribution patterns of each profile is given as results could not be printed out with the available software.

1. The profile obtained from Webb *et al.* (1984) did not match the descriptions of other authors; only small areas in Brazil, Angola, Congo, Ethiopia, Madagascar and two sites in Yunnan, China are shown as falling within this profile. The profile is therefore probably inaccurate as the natural distribution in China was not shown.

2. Areas satisfying the profile from Watts (1969) and Wu (1984) were more extensive. An upper limit of 35 ^{o}C was set for the mean temperature of the hottest month which was above the recorded mean temperature (30 ^{o}C), but below the recorded absolute temperature (44 ^{o}C). At 30 ^{o}C only three locations in China were included; by setting the limit to 35 ^{o}C the whole area of distribution in China was included. The discrepancy (between mean and absolute temperature excluding or including locations in China) may have been due to different sources of data.

Areas in Brazil (São Paulo, Minas Gerais, Paraná, Santa Catarina), Argentina (Misiones, Corrientes) were shown as suitable, closely corresponding to plantation locations and promising trial results (see section 2.1 above). In Africa an area enclosing much of Angola, parts along the borders of Zimbabwe and Congo, Congo and Tanzania, and much of northern Tanzania is suitable. Further north, central and southern Ethiopia and a small pocket in Uganda are also shown. All these areas appear to correspond with highland areas (above 1800 m). Central areas in Madagascar are considered suitable. An area along the east coast of South Africa (covering Cape Province, Natal and Transvaal)

is shown, it should be noted that this area is not the same as the trials given by Zwolinski (1988).

The last suitable area is the eastern coastline of Australia and extends from Queensland (at 24.5 °S, 151 °E) down to New South Wales (33.5 °S, 151 °E). As mentioned above trials were unsuccessful down to 28 °S due to a number of factors, drought being the only major climate factor. It is not known whether the species has been trialed in New South Wales.

3. When the profile representing good areas of production was modelled a much reduced area resulted. Sites were in Brazil (São Paulo, Minas Gerais) and scattered areas in Angola, Congo, Tanzania, Uganda, Kenya and Ethiopia. Madagascar was represented. There was a small area in Queensland from 24.5 to 27.0 °S.

4. Lower limits of mean temperature of the coldest month were set at 5 °C even though the summarised data indicated that mean temperature was 8 °C, the absolute minimum was -6 °C. As with profile 2 the lower limit was set to include sites within the area of best production. Other than China only a small area in Ethiopia and three locations in Queensland and New South Wales were shown.

5. The lower limit of temperature for the coldest month was set at 0 °C, although from the frost experiment (chapter VIII) it was known that the species is capable of surviving at -15 °C. When the lower limit was set at this level the results were identical indicating that other conditions were of more importance in affecting distribution (in this combination). As this profile was similar to profile 2 a similar distribution pattern was shown. There were some new sites; Mexico, Colombia, Korea (at the southern most tip) and Japan (southeast coast, possibly Tokyo).

6. This profile differs from profile 5 in rainfall pattern. The two New Zealand sites which have a uniform and slight winter distribution are included in this profile. The lower limit of mean annual rainfall was raised to an arbitrary level of 1000 mm in order to account for the change in rainfall distribution. Ten sites in the USA were shown (32.5 to 39.5 °N), these were situated in the eastern and southeastern states, mostly to the west and southwest of the Appalachian Mountains. Two sites were on the east coast; Baltimore (Maryland) and Richmond (Virginia). It is not known whether there have been any trials in the USA. In Brazil six locations in Paraná and Rio Grande do Sul are represented but these are in areas considered by Golfari as unsuitable due to frosting or water deficiencies.

In Australia suitable areas are found around the southern parts of the coast. In Western Australia there is a small coastal strip between Perth (32 °S, 116 °E) and Albany (35 °S, 117.5 °E). Another coastal strip in New South Wales extends from Newcastle (32.5 °S,

152 °E) to Berry (-35 °S, 150.5 °E). A narrow strip on the western side of the great divide in Victoria extends from Melbourne (38 °S, 145.5 °E) to Albury. In New Zealand sites from Dargaville (36 °S, 174 °E) to Atiamuri (38.5 °S, 176 °E) and Palmerston North (40.5 °S, 175.5 °E) were considered suitable.

4.3 Discussion

The reliability of the WORLD model is entirely dependant upon accurate climate data in both the stored locations and the input of climatic profile. Nevertheless it is useful as an indication of where it would be expected a species could be established. In profiles 2 and 5 the distribution of *C. lanceolata* in Brazil and Argentina is validated by field trials and plantings and thus it would be reasonable to expect that other areas shown in the world (in Africa and Australia) as suitable would be promising. This compares with the fact that the species was considered unsuitable in Queensland and southern Cape Province. While drought seems to have been a factor in *some* of the trials in Queensland other non climatic factors have also been in effect. Similarly in South Africa the trials in southern Cape Province were not part of the area considered suitable and Streets (1962) had earlier reported good growth of the species in the country (location not specified). It can therefore be assumed that profile 5 is a reasonable approximation of climatic requirements and the resulting world distribution is a good indication of the species potential (climatically).

Some caution must be applied when considering profile 6 however as rainfall patterns are quite different to that of its natural distribution. The areas deemed suitable in Brazil were considered unsuitable by Golfari (1970); trials have been carried out in some areas but there is no mention that the species has been tried in others. It is possible that the species has not been tried simply because of a perceived deficiency in some factor (climate or site). Frost damage due to continuous growth in winter (promoted by uniform rainfall) has been cited above; however this may be alleviated by site choice. In addition the New Zealand sites at New Plymouth and Rotorua exhibit winter and uniform rainfall patterns respectively as defined by Booth *et al.* (1989); however there is no evidence from either location that frost has seriously reduced growth. Furthermore growth is still seasonal in that resting buds are formed over winter months and are induced primarily by low temperature. This would suggest that uniform rainfall by itself does not promote continuous growth, but rather by an interaction with temperature or some other factor.

It is not known if the species has been tested in trials in Western Australia, Victoria or New South Wales. The most likely factor in limiting its distribution to coastal areas is rainfall, and this effectively restricts potential areas to those where other species are also suitable. In profile 6 the areas shown are also areas where *Pinus radiata* plantations are heavily concentrated (Lavery, 1986); it is therefore probable that while *C. lanceolata* may

be potentially suitable, it may not be a preferred species. Similarly there is no reference to the species being trialed in the USA.

The New Zealand sites are confined to the northern part of the North Island (Northland down to the Bay of Plenty regions) and one site at Palmerston North. As the WORLD model has only a few locations for New Zealand these results indicate that *C. lanceolata* is probably most suitable to these areas but not necessarily restricted to them. New Plymouth, for example, is not included although the climate there falls within the profile. Again the areas correspond to a large proportion of established *P. radiata* plantations.

5. NEW ZEALAND CLIMATE MODEL

The WORLD model is only useful in determining species suitability on a broad scale, as detailed interpolation surfaces were only available for Australia and Africa. The New Zealand Climate Model uses the BIOCLIM program to interrogate interpolated climate surfaces across New Zealand, a full description and outline of the model is given in Mitchell (1991). It is therefore a more accurate model compared to the WORLD model. As the model is the property of the University of Auckland, analysis was carried out by Dr Neil Mitchell from supplied data.

5.1 Methods

For the purposes of this study climate data from 16 stations in China taken from Watts (1969) and from the two sites in New Zealand where *C. lanceolata* is growing (see chapter XIII) were supplied to Dr Neil Mitchell. Climate data was then converted into climate profiles, with solar radiation being calculated from sunshine hour data (see Mitchell, 1991 for procedure). The following variables were calculated:

Temperature (^{o}C): Mean annual
Mean minimum of the coldest month *
Mean maximum of the hottest month *
Annual range
Seasonality
Mean of driest quarter (3 months) *
Mean of wettest quarter *

Solar radiation (MJ m^{-2} day^{-1}): Mean daily
Mean minimum of the coldest month *
Mean maximum of the hottest month *
Annual range
Seasonality
Mean of driest quarter *

Mean of wettest quarter *

Rainfall (mm): Mean annual *
Mean minimum of the driest month *
Mean maximum of the wettest month
Annual range
Seasonality
Mean of driest quarter *
Mean of wettest quarter *

* denotes key variables

The climatic profile is given in appendix H. The New Zealand database was then scanned for any site that fell within the profiles derived from either Chinese sites or New Zealand sites. Results were mapped for a conservative estimate based on all 21 variables and a reduced estimate based on 12 key variables.

5.2 Results

As with the WORLD model when the profile derived solely from Chinese data was used, no sites in New Zealand were suitable. This was due to the reversed seasonal patterns (summer versus winter or uniform rainfall). The climate profile was then extended to include the two New Zealand sites; other than altering rainfall patterns, the range of mean monthly temperature and solar radiation variables were extended at the minimum end (see appendix H). When this was done results showed that a range of sites in the North Island fell within the profile. Figure 15.1 shows the locations of the sites for conservative estimates using all 21 variables. The northern most sites were located near south Auckland (37 ^{o} 5' S), while the southern most were on the east coast around Wallingford and Blackhead (40 ^{o} 15 ' S). Sites were mainly concentrated in three large groups: Auckland-Hamilton, north Taranaki Bight-Wanganui, Wairoa-Napier. Other sites were more scattered through the East Cape, Bay of Plenty, and central North Island regions.

Using all 21 variables creates a precise but also restrictive profile and as with the earlier examples (section 3.2) a reduced dataset of 12 (key) variables was considered adequate to define a species' profile (Mitchell, pers. comm.). Results for the reduced dataset are mapped in Figure 15.2. The range of sites is extended from that of Figure 15.1 to include two sites in the Marlborough Sounds, more sites in the central North Island and Bay of Plenty region, and a greater concentration of sites around the south Taranaki Bight to Wanganui.

5. 3 Discussion

Results from the WORLD model gave three suitable sites, none of which match those from the New Zealand model. The results are not comparable however as different climate variables and a different number of variables were used, furthermore the WORLD model did not have many New Zealand climate stations in its database. The differences demonstrate the limits of modelling in deciding which variables and what number of variables are appropriate to predict a species' potential distribution. There is some validation of the model in that the Eastwood Hills Arboretum site was not supplied as data for the profile, yet this was predicted as suitable; height growth there was comparable to the Camp Huinga stand (chapter XIII).

In earlier studies four variables have been used to indicate marginal sites (Booth, 1985), while the WORLD model used six variables. In this instance 12 variables were considered as the important limiting factors distribution. Obviously there is a certain number of key variables limiting a species' distribution and as fewer variables are used, the results become less accurate and unsuitable sites may be deemed suitable. Conversely the more variables used, the more restrictive the results are and suitable sites can be underestimated (*i.e.* realised niche rather than fundamental niche).

It is apparent that *C. lanceolata* can grow at cooler (New Zealand) temperatures than those in China, and therefore other combinations of factors prevent its growth at lower temperatures in China. From the climate discussion in chapter III it would seem that at the northern and northwest limits both temperature and rainfall are lower compared with the more southern areas. In New Zealand the reversal of rainfall patterns is not necessarily limiting although drought sensitivity of the species would preclude sites with water deficits.

Notwithstanding this, the results show that climatically, *C. lanceolata* can be grown in New Zealand although it is restricted to the North Island and only in relatively few sites.

Table 15.1 Climatic Profiles of *C. lanceolata* From Various Authors

Source	Climate Variable					
	i)	ii)	iii)	iv)	v)	vi)
1	1100 - 1900	S	3.0 - 5.0	22.0 - 27.0	0.0 - 9.0	15.0 - 20.0
2	800 - 2100	S	0.0 - 5.0	24.7 - 35	0.1 - 15.2	14.8 - 22.2
3	1000 - 2000	S	1.3 - 4.3	28 - 30	5 - 13	16 - 21
4	1200 - 2000	S	0.0 - 3.3	28 - 30	5 - 10	18 - 20
5	800 - 2100	S	0.0 - 5.0	22 - 35	0 - 15.2	12 - 22.2
6	1000 - 2100	W, U	0.0 - 5.0	22 - 35	0 - 15.2	12 - 22.2

Dry season length for 3 and 4 are estimated from approximate growth period. Details of sources and climate variables are given in section 4.1.

Figure 15.1: Conservative Estimate of Site Locations For *C. lanceolata* in New Zealand (using 21 climate variables)

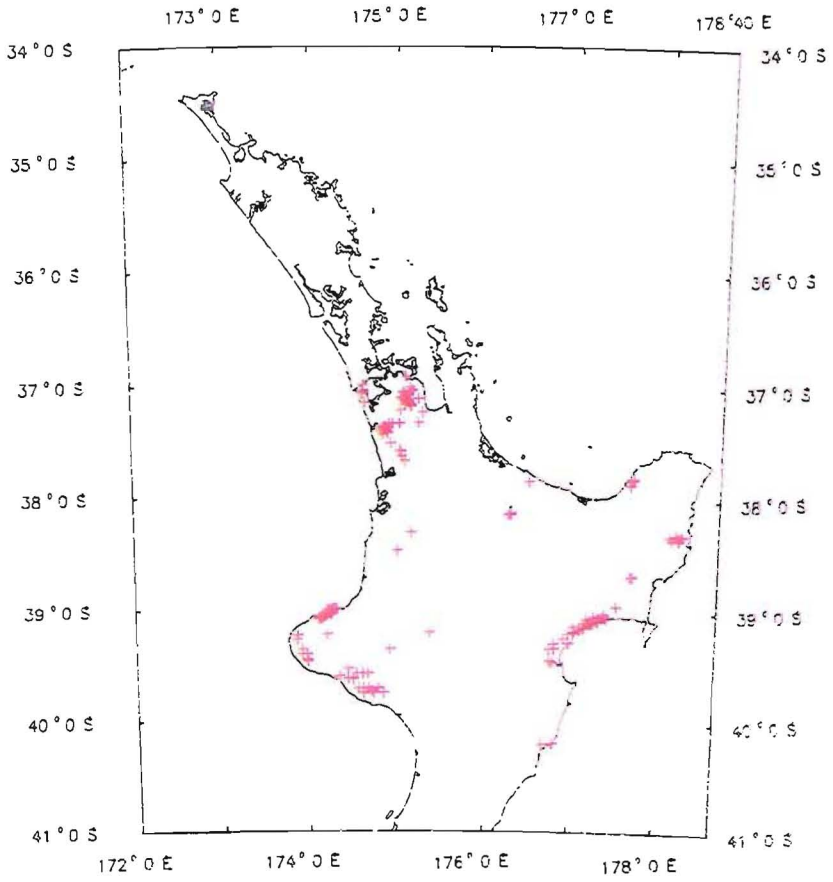
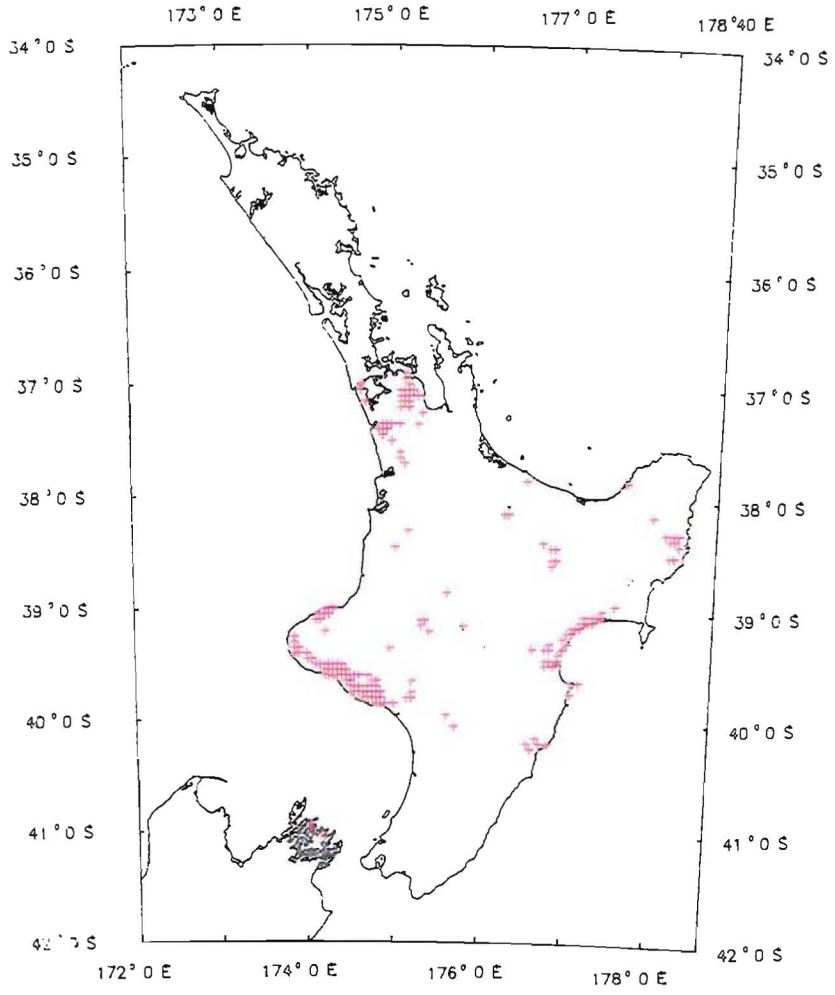


Figure 15.2: Reduced Dataset Estimate of Site Locations For *C. lanceolata* in New Zealand (using 12 climate variables)



CHAPTER XVI

REVIEW OF RESULTS AND CONCLUSIONS

While the range and scope of the experiments used in this study do not aim to explore the physiological attributes of *C. lanceolata* in full, they do serve to give an overall picture of the species' growth requirements, growth habit, and ability to withstand important environmental stresses. The aim of this thesis was to provide information on the prospects for growing *C. lanceolata* as a commercial forest tree species in New Zealand. The results from these experiments, together with the results from climate modelling and experience elsewhere, show that there is potential for *C. lanceolata* in New Zealand. The following is a review of the work carried out in this thesis, together with the findings from this study.

1. REVIEW

1.1 Reported Provenance Differences

Chapter III reviewed genetic research undertaken (primarily in China) to date. Significant differences between provenances have been consistently reported by a number of authors. Generally provenance variation was clinal and strongly related to temperature; in most trials the best performing provenances in terms of growth, frost resistance, and adaptability were those from the Nanling and Fujian areas of the central production zone. Isozyme studies have also shown a high degree of variability between populations.

These differences were not so apparent in this study. Isozyme analysis showed low levels of variability, both as a species and between provenances; while the nursery trial did not produce any significant differences in terms of second year height growth or bud burst. Length of growing season, as evidenced by date of bud set, did show some variation; with bud set being strongly correlated with latitude, mean annual temperature, mean temperature of the coldest month, and temperature sum. Thus there is some similarity with other studies in terms of the importance of temperature with respect to provenance variation.

In the physiological experiments there were observed differences between some provenances. These did not seem to be related to any environmental factor, and in at least one case, was most likely an artefact of the experiment. However a north - south trend was apparent, as with the nursery trial, in the requirement of winter chilling in order to

promote bud burst, with northern provenances producing less bud burst when little or no chilling was received.

The weight of the experimental evidence in this study suggests that, for the provenances used, there is little measurable provenance variation that can be related to any (meaningful) factor. A number of reasons as to this discrepancy with other studies have been suggested:

1) Provenance differences may become more apparent at older ages.

2) The long history of cultivation, with possible selection and seed exchange between regions, may have resulted in less variable populations.

3) Seed collection may have been from few or single trees from each stand.

Both 1) and 3) are more likely than 2). While the long cultivation of *C. lanceolata* may have resulted in seed exchange and selection for fast growth, nevertheless the consistency of findings in other studies along with the limited provenance variability found in this study imply that differences are real. As mentioned in the introduction there was no information available on seed collection for the study provenances. Seed collection from few trees would result in less variation as evidenced in the isozyme analysis; however it is possible that provenance differences in growth may still be apparent with such limited sampling, and this was not the case.

The nursery trial did not reveal any growth differences, although in part this could have been due to the frost damage at the end of the second growing season which was heaviest on the southern provenances which had not set bud. It is possible that at older ages (when the leading shoot is above the frost zone), differences in length of growing season may be apparent and result in provenance variation.

With respect to the findings of this study however the only observed difference of value is the degree of bud set at the end of the growing season, with the closely correlated degree of frost damage. In choosing provenances, northern provenances which set bud earlier are better suited to New Zealand conditions, and there is no evidence that their choice will result in a growth loss (at least at the nursery stage).

1.2 Species Response to Environmental Factors

Conditions in China that are considered optimal for growth have been described in chapter III. Climatic factors include: Mean annual rainfall 1200 mm or more; mean annual temperature of 16 - 19 ^{o}C; and 300 or more days with temperature above 5 ^{o}C (Hunan, FRI, pers. comm.). Site factors include: Deep, well drained and fertile soil; pH 4.5 - 6.5; shaded valleys and lower slopes of mountainous areas (FAO, 1982; Yang *et al.*, 1981; Zhang *et al.*, 1980).

C. lanceolata responds greatly to temperature. Significant differences were seen between low (18 and 20 °C) and high (28 °C) day temperatures, with greatest growth at 28 °C. This is closely related to the growth period; rapid growth occurs between June and September (Cai *et al.*, 1984) when mean monthly temperatures range from about 22 to 30 °C generally, and 25 - 30 °C in high yield areas (Wu, 1984). There are few sites in New Zealand which have mean monthly temperatures that high over summer.

Winter frost resistance in the species is adequate for most New Zealand sites and compares favourably with New Zealand podocarps and *P. radiata*. Hardiness values were -15.5 to -15.9 °C although this is only truly indicative of seedlings raised in Christchurch; other milder sites may result in lower hardiness values. Conversely findings in other studies suggest that shading may increase frost resistance, so there is a limited ability to manipulate frost resistance. *C. lanceolata* is very susceptible to out of season frosts however; a heavy frost of -5 °C can result in 100 % mortality. Lighter frosts in autumn (-0.5 to -3.5 °C) kill growing tips of seedlings that have not set bud. In choosing sites for the species, out of season frosts are likely to be a major limiting factor.

Water requirements are high. This is not unexpected, as the species is restricted to regions in China which do not experience water deficits (see chapter III). Growth was far greater when water was readily available at 100 % field capacity compared with lower water supplies at 30 and 15 % field capacity. New leaf growth was almost 50 % heavier for unstressed seedlings (100 % field capacity) than for stressed seedlings. Mortality was also greater at the lowest water level. Tolerance to low moisture levels can be developed in well established seedlings, but as with other species this is at the expense of growth. Recovery of stressed seedlings was apparent after two weeks of rewatering to field capacity; however photosynthesis rates were still significantly lower than those of unstressed seedlings, and conversely stomatal resistance was greater. This suggests that long term (morphological) change had resulted in stressed seedlings.

C. lanceolata has a high demand for nutrients. The nutrient experiment showed that nutrient deficiencies and poor growth occurred in seedlings grown on low nutrient levels (corresponding to 10.5 ppm N and lower). Greatest growth was found in high levels (210 ppm N) compared with other tree species; tissue analysis also revealed comparatively high levels of foliar concentrations. Mycorrhizal colonization resulted in greater seedling growth compared to seedlings that were non-mycorrhizal, although the response was only seen at high nutrient levels and was less significant than overall nutrient status. The needs for fertile soils and application of fertilisers were discussed in chapter III.

Light requirements were not separately examined in this study. Photosynthetic response to light intensities was examined in conjunction with temperature (chapter VII); temperature affected photosynthesis more than did light intensity. At 20 °C light

saturation was approached at approximately one-third of full sunlight (640 μE) while at 28 °C the response curve was still increasing. Light compensation point was low (20 μE) compared to *P. radiata* (39 μE). Seedling appearance was also greener when grown under 30 % shade cloth as opposed to full sunlight (chapter XI) where seedlings appeared yellowed. This and studies on *C. lanceolata*'s ecology suggest that the species prefers weak sunlight or low light intensities.

The combination of high nutrient and water requirement, low light compensation point, and preference for low light intensities are characteristics of shade tolerant species. In this respect *C. lanceolata* differs markedly from *P. radiata* which is a pioneer species.

1.3 Growth Patterns: Length, Dormancy, Phenology

The experiments described above deal with growth response to various environmental factors. Other experiments examined the growth pattern and habit of *C. lanceolata.* There is a definite seasonal pattern to shoot growth of the species; following bud burst in early September growth is typically sigmoid, growth slows down and ceases around April when buds are set. Resting buds formed over winter are small sized; from May through to August (winter) no height growth occurs until early September when buds begin to swell and burst again. The growing season in New Zealand is approximately 8 months; the small size of the bud suggests that predetermined growth is only a minor part of the total season's growth and free growth must therefore follow.

Mature (25 year old) trees, which would be expected to show the maximum or near maximum extent of predetermined growth, were sampled for first order buds close to the leading shoot. Leaf primordia counts were made and compared to the previous season's growth; mean tree estimates of predetermined growth as a proportion of total growth ranged from 0.24 to 0.49. Thus less than half of a season's shoot growth is predetermined. Free growth allows *C lanceolata* to maximise potential growing conditions while the predetermined component acts as a buffer against unfavourable years, in this respect the growth pattern is similar to the elliotii pattern of pine shoot growth.

A comparison of absolute growth showed that *C. lanceolata* was only half as tall as *P. radiata* at age 25 years. Over a short length of time and under good temperature, water and nutrient conditions, the relative growth rate of *C. lanceolata* seedlings was significantly faster than that of *P. radiata.* This would imply that *C. lanceolata* is an inherently faster growing species than *P. radiata* but that its resting growth phase does not allow it to grow seasonally for as long, and therefore that *P. radiata* is able to achieve greater absolute growth.

The induction of the resting phase appears to be regulated by low night temperature; photoperiod did not appear to influence induction of dormancy. Seedlings grown under an 8 hour daylength did not show any difference in growth to those under natural summer daylengths; temperature, water and nutrients were not limiting, and there was no sign of bud formation. However seedlings under high day (22 and 24 ^{o}C) and low night (9 and 7 ^{o}C) temperatures, and long (16 hour) photoperiod showed signs of winter resting after one month. Most seedlings had formed terminal resting buds and had adopted a brown winter colouration. All factors other than low night temperatures were conducive for growth; low night temperatures of 9 ^{o}C or less were therefore primarily responsible for bud set.

C. lanceolata does not exhibit true dormancy in the sense that chilling is required before growth resumes under favourable conditions. However chilling does significantly hasten bud burst. Those plants not subject to chilling took longer to burst bud compared with those that had experienced some chilling, when placed under warm conditions. The longer the chilling time the more rapid was bud burst. Provenance differences were noticed when no chilling or very light chilling was applied; however after long periods of chilling provenances all burst bud more or less immediately. This suggests that under natural New Zealand conditions all provenances would have experienced enough chilling so that rapid bud burst would result.

1.4 Wood Properties and Likely Pests

In addition to defining the species' requirements for (successful) growth, the presence of one 58 year old stand in New Plymouth and two 25 year old plots in Rotorua enabled a preliminary study on wood properties to be made. While the results are only truly indicative of the seed source, stand management and climate sampled, they do provide an estimation of what potential New Zealand grown *C. lanceolata* would be like. Physical, mechanical, and drying properties were examined.

Basic densities were lower than either much of the native grown (Chinese) *C. lanceolata* and considerably lower than *P. radiata* in New Zealand. The low basic density therefore resulted in lower strength values for mechanical properties (bending, compression, shear tests). However the strength values were similar to other (minor exotic) Taxodiaceae species *Sequoia sempervirens* and *Cryptomeria japonica*. Drying rates were very similar to *P. radiata* and air drying or drying under a conventional (high temperature) *P. radiata* kiln schedule produce very little degrade. One aspect not studied, but of interest when considering likely end uses, is the natural durability of the heartwood. This is probably due to the high extractive content, and components have been shown to inhibit fungi and termite attacks. The low strength and basic density of the timber makes *C. lanceolata* less suitable for structural uses than *P. radiata*, and more suited to end uses where strength is not important.

Other than environmental considerations, biotic factors are also important when assessing the introduction of a new species. A review in chapter II showed that a large number of pests and diseases have been documented for *C. lanceolata* in China. There appeared to be adequate control in most cases, through silvicultural, chemical, or biological means. No pest or disease was considered of large scale economic importance.

In Queensland trials, browse damage from opossum, wallaby, and rat was noted and was severe in some cases. The worst animal damage in China is by squirrels. Thus for the introduction of *C. lanceolata* to New Zealand, possible browse damage from the widespread opossum must be considered. Pen trials showed that there was a marked preference for *P. radiata* over *C. lanceolata* seedlings in the short term. However once *P. radiata* seedlings were eaten, *C. lanceolata* seedlings were than completely stripped over two nights. This suggests that damage at establishment may not initially be a problem, but that once opossums are familiar with *C. lanceolata* as a food source, damage may well increase.

1.5 Use as an Exotic and Climate Modelling

The species has been tried in a number of other countries although Brazil is the only country where it is grown in a commercial plantation situation. The lack of wide spread planting in these countries has been due to a variety of reasons. Frost damage was the most widely cited cause of failure of the species, especially in Europe and Latin America. Drought or water deficits were also responsible in some areas, other factors were poor site selection and animal browse.

Advanced computer climate models allow a species' climatic profile, where known, to be matched with a country's climate dataset and the identification of homoclimes; sites in the country which are similar or closely match the climatic profile. The advantages and disadvantages of this approach were discussed in chapter XV. Global modelling using the WORLD program developed by Dr Trevor Booth showed a variety of countries as suitable for *C. lanceolata*, including those where the species has been planted and trialed. New Zealand sites were considered suitable when both uniform and winter rainfall distributions were included. A more detailed model for New Zealand developed by Dr Neil Mitchell was next used to identify specific areas. Results showed that *C. lanceolata* was climatically suited to a restricted range of sites, almost exclusively in the North Island.

2. CONCLUSIONS

C. lanceolata is a fast growing tree under ideal conditions of high temperature, fertility, and rainfall, and as a seedling prefers conditions of weak sunlight. It is adapted to climates which have no water deficits, and very few out of season frosts; therefore its growth is largely regulated by temperature. There was little observed provenance variation in this experiment, but the lack of knowledge of the seed collection procedures prevents this finding from being conclusive for the species.

The experimental findings above suggest that while New Zealand conditions may not be optimal for growth, the species nevertheless has (limited) prospects for establishment in New Zealand. Provenance differences in growth were not found at the early seedling stage of growth; however selection of provenances in terms of short growing season may be advantageous in reducing early autumn frost damage. The factors most likely to limit growth potential in New Zealand are:

1) Lower temperatures in the growing season.
2) Out of season frosts.
3) Water deficits, especially during summer.
4) Low fertility sites or lack of fertiliser application.
5) Possible browse damage by opossums.

Results from climate modelling using a full dataset of 21 variables showed that *C. lanceolata* was climatically suited to a small number of sites throughout the North Island ranging from 37 ^{o} 5 ' S to 40 ^{o} 15 ' S, and mainly concentrated around three groups: Auckland-Hamilton, north Taranaki Bight-Wanganui, and Wairoa-Napier, with a smaller number of sites scattered in between. Use of a reduced dataset of 12 key variables resulted in heavier concentrations of sites in the above groups, slightly more sites in between and two sites in the Marlborough Sounds.

The climate model results agree with the findings from this study's experiments and furthermore, provides specific locations. Again, however, the identified sites must also be assessed for the limiting factors given above (with the exception of low temperatures during the growing season) and this may further reduce potential sites for the species.

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APPENDIX A: PROVENANCE DETAILS

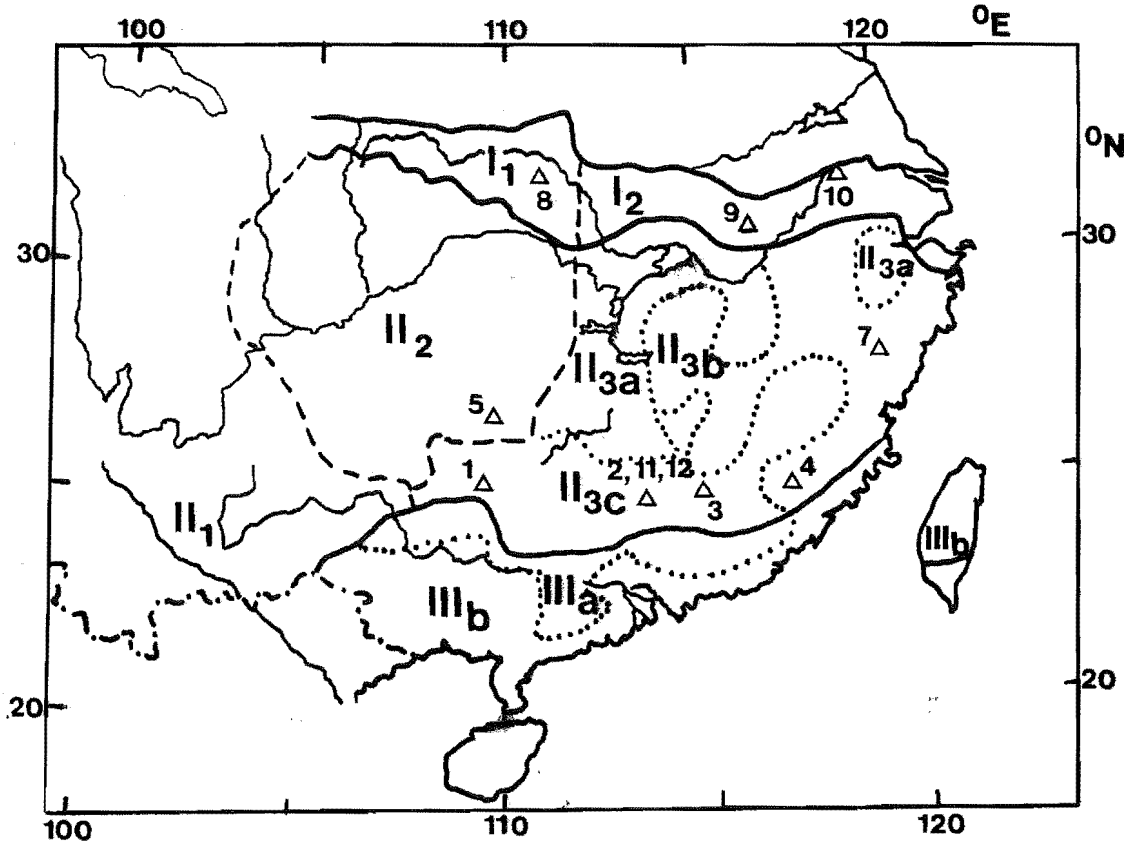
Provenance Origins (Province, location):

PV1	Guangxi, Rongshui	PV5	Hunan, Huitong	PV10	Jiangsu, Nanjing
PV2	Guangdong, Lechang	PV7	Zhejiang, Longquan	PV11	Guangdong, Lechang (green)
PV3	Jiangxi, Xinfeng Xian	PV8	Shaanxi, Pingli Xian	PV12	Guangdong, Lechang (blue)
PV4	Fujian, Datian Xian	PV9	Anhui, Huoshan		

	LAT (°N)	LON (°E)	ALT (m)	MAT (°C)	MCT (°C)	MWT (°C)	ACT (>10 °C)	MAR (mm)	MAS (hours)	FFD (days)
PV1	25	109	340	19.3	9.2	27.8	6205.3	1783.9	1382.7	235
PV2	25	113° 30'	200	19.7	9.2	28.3	6380.0	1436.0	1538.0	283
PV3	25	115	225	18.5	8.0	26.9	5926.9	1693.6	1691.0	290
PV4	25° 40'	118	400	18.9	9.1	27.1	5926.9	1532.6	1816.3	297
PV5	26° 50'	109° 45'	310	16.6	4.9	27.3	5171.1	1304.2	1462.7	280
PV7	28	119	320	17.6	6.5	27.6	5572.6	1699.4	1849.8	234
PV8	32° 30'	109° 45'	360-495	15.8	2.1	25.7	4248	943	1812	200
PV9	31° 30'	116	720	16.3	2.9	27.9	5143.3	1504.9	1954.9	200
PV10	32°	118° 45'	10	15.2	1.9	28.0	4860.1	1011.7	2151.5	202
PV11	25°	113° 30'	300	19.7	9.2	28.3	6380.0	1436.0	1538.0	283
PV12	25°	113° 30'	300	19.7	9.2	28.3	6380.0	1436.0	1538.0	283

See Chapter IV, section 2.3, or Appendix I for full names of climate varaiables. SEE ERRATA

APPENDIX B: *Cunninghamia lanceolata* PRODUCTION ZONES AND PROVENANCE LOCATIONS



Key:

___ Zone Boundary - - - Region Boundary . . . Sub-region Boundary

I_1 Northern zone, western region

I_2 Northern zone, eastern region

II_1 Central zone, western region

II_2 Central zone, central region

II_3 Central Zone, eastern region:

- II_{3a} Hill and plain sub-region
- II_{3b} Low mountain sub-region
- II_{3c} Mountain sub-region

III_a Southern zone, hill and mountain sub-region

III_b Southern zone, plateau sub-region

(From China, Cooperation Group of Chinese Fir, 1981b)

n.b. Refer to chapter III, section 3.1, for basis of the zones and regions.

APPENDIX C: SCIENTIFIC AND COMMON NAMES OF TREE SPECIES

Abies fraseri (Pursh) Poir.	Fraser fir
Acacia holosericea A. Cunn. ex. G. Don.	
Acacia mearnsii De Wild.	Black or tan wattle
Acer sacharrum Marsh.	Sugar maple
Alnus glutinosa (L,) Gaertn.	Black alder
Araucaria angustifolia	Parana pine
Araucaria cunninghamii	Hoop pine
Chamaecyparis obtusa (Sieb et Zucc.) Endl.	Hinoki cypress
Cornus stolonifora Michx.	Red-osier dogwood
Cryptomeria fortunei (also known as *Cryptomeria japonica* var. *sinensis*)	
Cryptomeria japonica (L. f.) D. Don	Japanese cedar (Sugi)
Cunninghamia lanceolata (Lamb.) Hook.	Chinese fir (China fir)
Cunninghamia konishii Hayata	Luanta fir
Cunninghamiostrobus geodertii Miller and Crabtree	
Dacrycarpus dacrydioides (A. Rich.) de Laub.	Kahikatea
Dacrydium cupressinum Lamb.	Rimu
Erythrophleum fordii	
Eucalyptus citiodora Hook.	Lemon-scented gum
Eucalyptus nitens (Deane et Maiden) Maiden	Shining gum
Eucalyptus regnans F. Mueller	Mountain ash
Fokienia sp.	
Glyptostrobus sp.	Chinese swamp cypress
Keteleeria spp.	
Larix dahurica Turcz	Dahurian larch
Larix laricina (Du Roi) K. Koch	Tamarack
Larix leptolepis (Sieb. and Zucc.) Murr.	Larch
Larix occidentalis Nutt.	Western larch
Larix potaninii Batal.	Chinese larch
Lagarastrobus colensoi (Hook.) Quinn	Silver pine
Lepidothamnus intermedius (Kirk) Quinn	Yellow-silver pine
Libocedrus macrolepis (now called *Calocedrus macrolepis*)	
Liriodendron spp.	Tulip tree
Magnolia spp.	Magnolia
Michelia macclurei	Homana

Paulownia tomentosa Steud.	Royal paulownia
Phyllocladus alpinus Hook. f.	Mountain toatoa
Picea abies (L.) Karst.	Norway spruce
Picea engelmannii Parry	Engelmann spruce
Picea mariana(Mill.) B. S. P.	Black spruce
Picea sitchensis (Bong.) Carr.	Sitka spruce
Pinus aristata Engelm.	Rocky mountain bristlecone pine
Pinus attenuata Lemm.	Knobcone pine
Pinus banksiana Lamb.	Jack pine
Pinus brutia Ten.	Erectcone pine (Calabrian pine)
Pinus caribaea Morelet	Caribbean pine
Pinus contorta Dougl.	Lodgepole pine
Pinus elliottii Engelm.	Slash pine
Pinus massoniana Lamb.	Masson pine
Pinus pinaster Ait.	Maritime pine
Pinus radiata D. Don	Radiata pine
Pinus rigida Mill.	Pitch pine
Pinus resinosa Ait.	Red pine (Norway pine)
Pinus sabiniana Dougl.	Digger pine
Pinus sylvestris L.	Scots pine (Scotch pine)
Pinus strobus L.	Eastern white pine
Pinus taeda L.	Loblolly pine
Pinus virginiana Mill.	Virginia pine
Populus deltoides Bartr.	Eastern cottonwood
Pseudotsuga menziesii (Mirb.) Franco	Douglas fir
Quercus rubra L.	Northern red oak (Eastern red oak)
Robinia pseudoacacia L.	Black locust
Salix nigra Marsh.	Black willow
Sassafras tsumu (tzumu)	Sassafras
Schima wallichi	
Sequoia sempervirens (D. Don) Endl.	Redwood
Sequoiadendron giganteum (Lindl.) Buchh.	Giant sequoia (Big tree)
Taiwania cryptomerioides Hayata	Taiwania
Taxodium distichum (L.) Rich	Bald cypress
Thuja occidentalis L.	Northern white cedar
Thuja plicata Donn	Western red cedar
Tsuga canadensis Carr.	Eastern hemlock
Tsuga heterophylla Sarg.	Western hemlock
Ulmus americana L.	American elm

APPENDIX D.1: ISOZYME RECIPES - Extraction Buffer and Starch Gel

Note: More detailed explanation of isozyme procedures and modification of recipes are given in Wendel and Weeden (1989).

Aspen Extraction Buffer:	50 ml	0.1M Tris
	0.100 g	Ascorbic Acid
	0.047 g	Cysteine
	8.55 g	Sucrose
	0.5 ml	Tween
	1 ml	MgCl (10%)
	1 ml	CaCl (10%)
	2 drops	β-mercaptoethanol
	pH to 7.5 with HCl (approximately 8 drops)	

Histidine Buffer System

Electrode Buffer:	1 l	Deionised distiled water
	0.125M	Tris (15.135 g l^{-1})
	adjust pH to 7.0 with 1M citric acid (approximately 25 ml)	
Gel Buffer:	1 l	Deionised distiled water
	0.014M	L-Histidine (2.1 g l^{-1})
	0.002M	EDTA (0.08 g l^{-1})
	adjust pH to 7.0 with 1.0M Tris (approximately 8 ml)	

Poulik Buffer System

Electrode Buffer:	0.3M	Boric acid (19.16 g l^{-1})
	0.063M	Sodium hydroxide (2.52 g l^{-1})
	adjust pH to 8.1 with NaOH	
Gel Buffer:	0.08M	Tris (9.68 g l^{-1})
	0.009M	Citric acid
	adjust pH to 8.65 with HCl before use	

APPENDIX D.2: ISOZYME RECIPES - Enzyme Stains

Enzyme nomenclature listed as acronym: colloquial name, and enzyme commission number (E.C.)

AAT: Aspartate aminotransferase (or GOT: Glutamic-oxaloacetic trans aminase), E.C. 2.6.1.1

25 ml	0.2M Tris-HCl pH8.0	
25 ml	AAT substrate solution	
	(500 ml	Distiled water
	14.2 g	Sodium Phosphate, dibasic
	5.0 g	PVP-40T
	1.33 g	L-Aspartic acid
	0.5 g	EDTA
	0.365 g	α-ketoglutaric acid)
0.1 g	Fast blue BB	

incubate at 37 °C in the dark for 30 minutes

ACON: Aconitase, E.C.4.2.1.3

40 ml	0.2M Tris-HCl pH 8.0
2 ml	NADP (1 %)
1 ml	PMS (1 %)
1 ml	NBT (1 %)
1 ml	MgCl (10 %)
0.25 g	Cis-aconitic acid (or 5 ml of 5 % soln., pH 7.0)
40 units	IDH

incubate at 37 °C in the dark

ADH: Alcohol dehydrogenase, E.C.1.1.1.1

25 ml	0.2M Tris-HCl pH 8.0
1 ml	NAD (1 %)
1 ml	PMS (1 %)
1 ml	NBT (1 %)
2.5 ml	Absolute ethanol

incubate in the dark

APH: Acid phosphotase (or ACP), E.C.3.1.3.2

25 ml	Na-acetate 0.2M pH 5.0 (adjust with acetic acid)
0.5 ml	MgCl (10 %)
75 mg	Na-α-napthyl acid phosphotase
38 mg	Fast Garnet GBC salt

DIA: Diaphorase, E.C.1.6.4.3

50 ml	0.2M Tris-HCl ph 8.0
1 mg	2,6-dichlorophenol indophenol
12.5 mg	NADH
stir for a couple of minutes then add	
1 ml	MTT (1 %)
incubate at	37 °C for 30 minutes

EST: Esterase, E.C.3.1.1.-

50 ml	0.2M Phosphate buffer pH 6.4
50 mg	α-napthyl acetate dissolved in acetone
50 mg	β-napthyl acetate dissolved in acetone
100 mg	Fast Blue RR salt
incubate at room temperature in the dark for 60 minutes	

G6PDH: Glucose-6-phosphate dehydrogenase, E.C.1.1.1.49

25 ml	0.2M Tris-HCl ph 8.0
1 ml	NADP (1 %)
0.5 ml	MTT (1 %)
0.5 ml	PMS (1 %)
0.5 ml	MgCl (10 %)
100 mg	D-glucose-6-phosphate
incubate at 37 °C in the dark	

IDH: Isocitrate dehydrogenase, E.C.1.1.1.42

25 ml	0.2M Tris-HCl ph 8.0
0.5 ml	NADP (1 %)
0.5 ml	PMS (1 %)
0.5 ml	NBT (1 %)
0.5 ml	MgCl (10 %)
100 mg	DL-Isocitric acid
incubate at 37 °C in the dark	

MDH: Malate dehydrogenase, E.C.1.1.1.37

25 ml	0.2M Tris-HCl ph 8.0
25 ml	2.0M Sodium malate solution pH 7.0
	(13.4 g L. Malic acid
	10.5 g Sodium carbonate
	500 ml distiled water)
1 ml	NADP (1 %)
0.5 ml	PMS (1 %)
0.5 ml	NBT (1 %)
incubate at 37 °C in the dark	

ME: Malic enzyme (or $NADP^+$: Malate dehydrogenase), E.C. 1.1.1.40

25 ml	0.2M Tris-HCl ph 8.0
25 ml	2.0M Sodium malate solution pH 7.0
0.5 ml	NADP (1 %)
0.5 ml	PMS (1 %)
1 ml	NBT (1 %)
0.5 ml	MgCl (10 %)

MR: Menadione reductase (or NAD[p]DH: NAD[P]H dehydrogenase), E.C.1.6.99.2

50 ml	0.2M Tris-HCl ph 8.0
17 mg	Menadione
17 mg	NADH
1 ml	NBT (1 %)
incubate at 37 °C in the dark	

6PG: 6-Phosphogluconate dehydrogenase (or PGD), E.C.1.1.1.44

20 ml	0.2M Tris-HCl ph 8.0
2 ml	NADP (1 %)
2 ml	PMS (1 %)
2 ml	MTT (1 %)
2 ml	MgCl (10 %)
10 mg	6-Phosphogluconic acid
incubate at 37 °C in the dark	

PER: Peroxidase (or PRX), E.C.1.11.1.7

46 ml	Na-acetate 0.2M pH5.0 (adjust with acetic acid)
1 ml	Hydrogen peroxide (5 %)
1 ml	CaCl (0.1M)
25 mg	3-amino-9-ethyl carbazole dissolved in 2.5 ml dimethyl formamide

PGI: Phosphoglucose isomerase (or GPI: Glucose-6-phosphate isomerase), E.C.5.3.1.9

25 ml	0.2M Tris-HCl ph 8.0
0.5 ml	NADP (1 %)
0.5 ml	PMS (1 %)
0.5 ml	MTT (1 %)
0.5 ml	MgCl (10 %)
10 units	G-6-PDH
13 mg	Fructose-6-phosphate

incubate at 37 °C in the dark

PGM: Phosphoglucomutase, E.C.5.4.2.2 (formerly 2.7.5.1)

25 ml	0.2M Tris-HCl ph 8.0
0.5 ml	NADP (1 %)
0.5 ml	PMS (1 %)
0.5 ml	MTT (1 %)
0.5 ml	MgCl (10 %)
10 units	G-6-PDH
1 ml	Glucose-1,6-doiP (0.01 %)
150 mg	Glucose-1-phosphate

incubate at 37 °C in the dark

SOD: Superoxide dismutase, E.C.1.15.1.1

50 ml	0.2M Tris-HCl ph 8.0
0.5 ml	NBT
2 mg	Riboflavin
148 mg	EDTA

place over light and watch, fix when loci appear

APPENDIX E: MODIFIED HALF STRENGTH HOAGLAND'S SOLUTION

	Molecular Weight (g)	Concentration (g l^{-1}) Stock	Final		ppm
Stock Solution A					
Calcium nitrate				Ca	100.20
$Ca(NO_3)_2.4H_20$	236.15	295.19	0.59038	N	70.04
10 % EDTA NaFe	367.05	6.83	0.0208	Fe	2.08
				Na	0.86
Stock Solution B					
Potassium phosphate				K	19.55
KH_2PO4	136.08	34.02	0.06804	P	15.49
Potassium nitrate				K	97.75
KNO_3	101.11	126.39	0.25278	N	35.06
Stock solution C					
Magnesium sulfate				Mg	24.32
$MgSO_4.7H_2O$	246.5	123.24	0.24648	S	32.06
Boric acid				B	0.250
H_3BO_3	61.82	0.715	0.00143		
Manganese chloride				Mn	0.251
$MnCl_2.4H_2O$	197.92	0.4525	0.000905	Cl	0.324
Zinc sulfate				Zn	0.025
$ZnSO_4.7H_2O$	287.55	0.055	0.000110	S	0.012
Copper sulfate				Cu	0.010
$CuSO_4.5H_2O$	249.68	0.020	0.00004	S	0.005
Sodium molybdate				Na	0.003
$Na_2MoO_4.2H_2O$	241.93	0.0067	0.0000134	Mo	0.005
Potassium chloride				K	1.652
KCl	74.56	1.575	0.00315	Cl	1.498

As per DSIR, Palmerston North, Plant Physiology Section, Climate Laboratory. The standard solution is comprised of:

(2 ml of stock A + 2 ml of stock B + 2 ml stock C) / 1 litre of distiled water

This gives a standard (half strength Hoagland's) solution which corresponds to NL100 in chapter X. For higher NL's amount of stock solutions were increased as appropriate; stock solution C (micro nutrients) was kept at a constant 2 ml (*e.g.* for NL200, 4 ml of each stock solutions A and B, and 2 ml of stock solution C were diluted in 1 litre of distiled water).

For lower NL's further dilution was carried out for stock solutions A and B, with stock solution C being added at the end (*e.g.* for NL5, 0.2 ml of stock solutions A and B were diluted in 2 litres of distiled water, and 2 ml of stock solution C was then added).

APPENDIX F: FAA SOLUTION RECIPE

Recipe for 1 litre of Formalin acetic acid (FAA) solution, can be stored at room temperature or in fridge.

605 ml	Distilled water
315 ml	Ethanol (50 %)
30 ml	Formaldehyde (37 %)
50 ml	Glacial acetic acid

Length of material to be fixed with FAA can be up to 5 cm. Material should be placed in fixative as soon as possible after cutting and evacuated in a vacuum for 6 hours.

APPENDIX G.1: MECHANICAL TEST RESULTS

Bending Test

Air Dried:

Sample	Proportional Limit				Failure	
	Load (kN)	Deflection (mm)	MOE (MPa)	Stress (MPa)	Load (kN)	MOR (MPa)
E.4.1	0.60	3.20	6431.25	31.50	0.92	48.30
E.4.2	0.50	2.60	6596.15	26.25	0.86	45.15
E.4.3	0.48	2.20	7483.64	25.20	0.78	40.95
E.4.4	0.60	2.70	7622.22	31.50	0.93	48.83
W.4.1	0.52	4.00	4459.00	27.30	0.75	39.38
W.4.2	0.50	2.60	6596.15	26.25	0.80	42.00
W.4.3	0.52	2.90	6150.34	27.30	0.84	44.10
W.4.4	0.49	2.30	7307.39	25.73	0.86	45.15
E.9.1	0.66	3.80	5957.37	34.65	0.92	48.30
E.9.2	0.50	2.40	7145.83	26.25	0.90	47.25
E.9.3	0.66	2.90	7806.21	34.65	1.07	56.18
W.9.1	0.66	3.20	7074.38	34.65		
W.9.2	0.64	3.40	6456.47	33.60	0.95	49.88
W.9.2	0.58	3.20	6216.88	30.45	0.86	45.15
W.9.3	0.60	2.50	8232.00	31.50	1.06	55.65
E.14.1	0.62	4.10	5186.83	32.55	0.85	44.63
E.14.2	0.73	3.50	7154.00	38.33	1.04	54.60
E.14.3	0.70	2.90	8279.31	36.75	1.12	58.80
W.14.1	0.66	3.60	6288.33	34.65	0.98	51.45
W.14.2	0.62	3.30	6444.24	32.55	0.97	50.93
W.14.3	0.58	2.60	7651.54	30.45		
W.14.4	0.66	2.70	8384.44	34.65	1.09	57.23
E.41.1	0.60	2.10	9800.00	31.50	1.03	54.08
E.41.2	0.85	3.10	9404.84	44.63	1.28	67.20
E.41.3	0.54	1.90	9748.42	28.35	1.20	63.00
W.41.1	0.64	2.80	7840.00	33.60		
W.41.2	0.66	2.60	8706.92	34.65	1.10	57.75
W.41.3	0.73	2.70	9273.70	38.32		
Sample		Proportional Limit			Failure	

	Load (kN)	Deflection (mm)	MOE (MPa)	Stress (MPa)	Load (kN)	MOR (MPa)
E.42.1	0.61	2.90	7214.83	32.03		
E.42.2	0.55	2.80	6737.50	28.88	0.94	49.35
E.42.3	0.70	3.30	7275.76	36.75	1.10	57.75
E.42.4	0.80	3.80	7221.05	42.00	1.11	58.28
W.42.2	0.60	2.80	7350.00	31.50	0.92	48.30
W.42.3	0.53	2.30	7903.91	27.83	0.94	49.35
W.42.4	0.78	3.00	8918.00	40.95		
average	0.62	2.94	7433.08	32.51	0.97	51.00
sd	0.09	0.54	1219.87	4.79	0.13	6.75
max.	0.85	4.10	9800.00	44.63	1.28	67.20
min.	0.48	1.90	4459.00	25.20	0.75	39.38

Green:

Sample	Proportional Limit				Failure	
	Load (kN)	Deflection (mm)	MOE (MPa)	Stress (MPa)	Load (kN)	MOR (MPa)
E.4.1	0.37	2.70	4700.37	19.43	0.61	32.03
E.4.2	0.44	2.70	5589.63	23.10	0.66	34.65
E.4.3	0.36	2.30	5368.70	18.90	0.59	30.98
E.4.4	0.40	2.60	5276.92	21.00	0.63	33.08
W.4.1	0.40	3.30	4157.58	21.00	0.61	32.03
W.4.2	0.39	2.60	5145.00	20.48	0.66	34.65
W.4.3	0.44	2.60	5804.62	23.10	0.66	34.65
W.4.4	0.34	2.40	4859.17	17.85	0.51	26.78
E.9.1	0.45	2.80	5512.50	23.63	0.69	36.23
E.9.2	0.46	2.50	6311.20	24.15	0.69	36.23
E.9.3	0.46	2.30	6860.00	24.15	0.76	39.90
W.9.1	0.38	3.70	3522.70	19.95	0.53	27.83
W.9.2	0.46	2.80	5635.00	24.15	0.69	36.23
W.9.3	0.42	2.50	5762.40	22.05	0.70	36.75
E.14.1	0.40	2.80	4900.00	21.00	0.66	34.65
E.14.2	0.50	2.90	5913.79	26.25	0.80	42.00
E.14.3	0.50	2.70	6351.85	26.25	0.75	39.38
Sample		Proportional Limit			Failure	

	Load (kN)	Deflection (mm)	MOE (MPa)	Stress (MPa)	Load (kN)	MOR (MPa)
E.14.3	0.51	2.60	6728.08	26.78	0.76	39.90
W.14.1	0.45	3.80	4061.84	23.63	0.62	32.55
W.14.2	0.50	2.80	6125.00	26.25	0.78	40.95
W.14.3	0.46	2.50	6311.20	24.15	0.79	41.48
W.14.4	0.48	2.20	7483.64	25.20	0.84	44.10
E.41.1	0.40	3.00	4573.33	21.00	0.65	34.13
E.41.2	0.53	2.50	7271.60	27.83	0.86	45.15
E.41.3	0.50	2.20	7795.45	26.25	0.89	46.73
W.41.1	0.44	3.20	4716.25	23.10	0.67	35.18
W.41.2	0.60	2.60	7915.38	31.50	0.94	49.35
W.41.3	0.48	1.80	9146.67	25.20	0.97	50.93
E.42.1	0.48	2.70	6097.78	25.20	0.78	40.95
E.42.2	0.52	3.20	5573.75	27.30	0.78	40.95
E.42.3	0.64	3.50	6272.00	33.60	0.95	49.88
E.42.4	0.57	3.10	6306.77	29.93	0.84	44.10
E.42.4	0.54	3.20	5788.13	28.35	0.77	40.43
W.42.2	0.50	2.60	6596.15	26.25	0.80	42.00
W.42.3	0.52	2.40	7431.67	27.30	0.93	48.83
W.42.4	0.56	2.40	8003.33	29.40	0.87	45.68
average	0.47	2.67	6033.40	24.57	0.74	38.92
sd	0.07	0.43	1224.78	3.59	0.12	6.22
max.	0.64	3.80	9146.67	33.60	0.97	50.93
min.	0.34	1.80	3522.70	17.85	0.51	26.78

Compression (Parallel to the Grain) Test

Air Dried:

Sample	Proportional Limit				Maximum	
	Load (kN)	Deflection (mm)	MOE (MPa)	Stress (MPa)	Failure (kN)	MCS (MPa)
E.4.1	8.00	0.25	960.00	20.00	9.90	24.75
E.4.2	8.60	0.30	860.00	21.50	9.90	24.75
E.4.4	9.00	0.35	771.43	22.50	10.70	26.75
W.4.1	8.60	0.30	860.00	21.50	9.30	23.25
W.4.2	7.40	0.20	1110.00	18.50	10.20	25.50
W.4.3	6.80	0.45	453.33	17.00	9.00	22.50
W.4.4	5.80	0.30	580.00	14.50	9.30	23.25
E.9.1	8.40	0.35	720.00	21.00	9.60	24.00
E.9.2	6.60	0.25	792.00	16.50	10.00	25.00
E.9.3	9.80	0.30	980.00	24.50	12.00	30.00
W.9.1	8.00	0.30	800.00	20.00	10.50	26.25
W.9.2	6.00	0.25	720.00	15.00	10.00	25.00
W.9.2	8.00	0.30	800.00	20.00	11.10	27.75
W.9.3	7.80	0.30	780.00	19.50	11.50	28.75
E.14.1	7.60	0.30	760.00	19.00	10.70	26.75
E.14.2	10.00	0.35	857.14	25.00	11.90	29.75
E.14.3	10.60	0.30	1060.00	26.50	13.00	32.50
E.14.4	10.40	0.30	1040.00	26.00	12.50	31.25
W.14.1	7.40	0.25	888.00	18.50	10.90	27.25
W.14.2	8.40	0.20	1260.00	21.00	10.60	26.50
W.14.3	11.20	0.35	960.00	28.00	12.70	31.75
W.14.4	9.00	0.25	1080.00	22.50	12.40	31.00
E.41.1	7.00	0.20	1050.00	17.50	12.50	31.25
E.41.2	10.00	0.35	857.14	25.00	14.00	35.00
E.41.3	10.00	0.30	1000.00	25.00	15.00	37.50
W.41.1	7.80	0.25	936.00	19.50	11.80	29.50
W.41.2	9.60	0.45	640.00	24.00	13.40	33.50
W.41.3	9.80	0.30	980.00	24.50	14.30	35.75
E.42.1	7.80	0.40	585.00	19.50	11.30	28.25
E.42.2	7.40	0.25	888.00	18.50	11.10	27.75
E.42.3	8.80	0.30	880.00	22.00	12.90	32.25
E.42.4	8.60	0.30	860.00	21.50	12.30	30.75
W.42.1	7.00	0.30	700.00	17.50	11.30	28.25

Sample	Proportional Limit				Maximum	
	Load (kN)	Deflection (mm)	MOE (MPa)	Stress (MPa)	Failure (kN)	MCS (MPa)
W.42.2	8.40	0.45	560.00	21.00	11.30	28.25
W.42.3	7.00	0.45	466.67	17.50	11.70	29.25
W.42.4	10.60	0.35	908.57	26.50	14.00	35.00
average	8.42	0.31	844.54	21.06	11.52	28.79
sd	1.36	0.07	182.26	3.41	1.52	3.79
max.	11.20	0.45	1260.00	28.00	15.00	37.50
min.	5.80	0.20	453.33	14.50	9.00	22.50

Green:

Sample	Proportional Limit				Maximum	
	Load (kN)	Deflection (mm)	MOE (MPa)	Stress (MPa)	Failure (kN)	MCS (MPa)
E.4.1	5.50	0.25	660.00	13.75	6.20	15.50
E.4.2	4.90	0.25	588.00	12.25	6.75	16.88
E.4.3	5.00	0.35	428.57	12.50	5.60	14.00
E.4.4	5.40	0.25	648.00	13.50	6.35	15.88
W.4.1	6.00	0.30	600.00	15.00	6.70	16.75
W.4.2	5.40	0.25	648.00	13.50	6.55	16.38
W.4.3	5.00	0.35	428.57	12.50	6.10	15.25
W.4.4	4.40	0.25	528.00	11.00	5.30	13.25
E.9.1	5.70	0.20	855.00	14.25	6.65	16.63
E.9.2	6.20	0.25	744.00	15.50	7.00	17.50
E.9.3	6.90	0.25	828.00	17.25	7.70	19.25
W.9.1	5.50	0.20	825.00	13.75	6.70	16.75
W.9.2	4.00	0.15	800.00	10.00	6.05	15.13
W.9.3	6.40	0.30	640.00	16.00	7.15	17.88
E.14.1	6.00	0.20	900.00	15.00	7.00	17.50
E.14.2	6.40	0.25	768.00	16.00	6.70	16.75
E.14.3	7.10	0.30	710.00	17.75	7.55	18.88
E.14.4	8.00	0.30	800.00	20.00	8.50	21.25
W.14.1	7.00	0.25	840.00	17.50	7.50	18.75
W.14.2	8.00	0.30	800.00	20.00	8.50	21.25
W.14.3	7.50	0.35	642.86	18.75	8.20	20.50

Sample	Proportional Limit				Maximum	
	Load (kN)	Deflection (mm)	MOE (MPa)	Stress (MPa)	Failure (kN)	MCS (MPa)
W.14.4	7.40	0.25	888.00	18.50	8.20	20.50
E.41.1	6.30	0.25	756.00	15.75	7.55	18.88
E.41.2	8.50	0.35	728.57	21.25	9.80	24.50
E.41.3	9.00	0.30	900.00	22.50	9.40	23.50
W.41.1	6.80	0.25	816.00	17.00	7.50	18.75
W.41.2	8.30	0.30	830.00	20.75	9.20	23.00
W.41.3	9.60	0.35	822.86	24.00	10.40	26.00
E.42.1	7.80	0.25	936.00	19.50	8.20	20.50
E.42.2	7.00	0.40	525.00	17.50	8.10	20.25
E.42.3	8.20	0.25	984.00	20.50	9.40	23.50
E.42.4	8.40	0.25	1008.00	21.00	9.20	23.00
W.42.1	8.30	0.30	830.00	20.75	8.80	22.00
W.42.2	6.90	0.30	690.00	17.25	7.70	19.25
W.42.3	8.10	0.30	810.00	20.25	9.00	22.50
W.42.4	8.10	0.30	810.00	20.25	8.85	22.13
average	6.81	0.28	750.46	17.01	7.67	19.17
sd	1.39	0.05	141.60	3.47	1.26	3.15
max.	9.60	0.40	1008.00	24.00	10.40	26.00
min.	4.00	0.15	428.57	10.00	5.30	13.25

Shear (Parallel to the Grain) Test

	Air Dried				Green			
	Load (kN)		Stress (MPa)		Load (kN)		Stress (MPa)	
Sample	1	2	1	2	1	2	1	2
E.4.1	3.26	3.47	8.15	8.68	2.50	2.40	6.25	6.00
E.4.2	2.87	3.20	7.18	8.00	1.89	1.76	4.73	4.40
E.4.3	2.23	2.00	5.58	5.00	1.47	1.54	3.68	3.85
E.4.4	2.50	2.60	6.25	6.50	1.62		4.05	
W.4.1	4.68	4.15	11.70	10.38	2.80	2.75	7.00	6.88
W.4.2	3.30	2.75	8.25	6.88	2.10	2.15	5.25	5.38
W.4.3	2.24	2.35	5.60	5.88	2.08	2.17	5.20	5.43
W.4.4	2.20	2.00	5.50	5.00	1.55	1.90	3.88	4.75
E.9.1	3.98	3.80	9.95	9.50	1.82	1.77	4.55	4.43

	Air Dried				Green			
	Load (kN)		Stress (MPa)		Load (kN)		Stress (MPa)	
Sample	1	2	1	2	1	2	1	2
E.9.2	2.70	2.93	6.75	7.33	2.05	2.00	5.13	5.00
E.9.3	3.25	3.40	8.13	8.50	2.13	2.17	5.33	5.43
W.9.1	3.27	3.24	8.18	8.10	2.96	2.90	7.40	7.25
W.9.2	2.42	3.05	6.05	7.63	1.81	1.85	4.53	4.63
W.9.2	2.55	2.37	6.38	5.93				
W.9.3	3.10	3.26	7.75	8.15	1.94	1.96	4.85	4.90
E.14.1	3.00	3.10	7.50	7.75	2.37	2.28	5.93	5.70
E.14.2	4.07	4.52	10.18	11.30	2.40		6.00	
E.14.3	3.65	3.88	9.13	9.70	2.15	2.06	5.38	5.15
E.14.4	3.50	3.88	8.75	9.70	2.30	2.26	5.75	5.65
W.14.1	3.55	3.14	8.88	7.85	2.25	2.01	5.63	5.03
W.14.2	4.50	4.05	11.25	10.13	2.59	2.51	6.48	6.28
W.14.3	2.95	3.35	7.38	8.38	2.35	2.27	5.88	5.68
W.14.4	3.20	3.00	8.00	7.50	2.10	2.06	5.25	5.15
E.41.1	2.44	3.04	6.10	7.60	3.56	2.95	8.90	7.38
E.41.2	3.05	2.66	7.63	6.65	1.95	1.85	4.88	4.63
E.41.3	3.00	2.80	7.50	7.00	2.55	2.30	6.38	5.75
W.41.1	1.85	3.13	4.63	7.83	2.26	2.50	5.65	6.25
W.41.2	2.72	2.28	6.80	5.70	2.13	2.19	5.33	5.48
W.41.3	2.75	2.56	6.88	6.40	2.21	2.43	5.53	6.08
E.42.1	2.76	3.15	6.90	7.88	2.83	2.55	7.08	6.38
E.42.2	4.07	3.70	10.18	9.25	2.77	2.35	6.93	5.88
E.42.3	3.45	3.13	8.63	7.83	2.67	2.76	6.68	6.90
E.42.4	3.01	2.97	7.53	7.43	2.17	2.19	5.43	5.48
W.42.1	3.48	3.16	8.70	7.90	3.34	2.88	8.35	7.20
W.42.2	2.73	2.85	6.83	7.13	2.02	2.09	5.05	5.23
W.42.3	3.03	2.81	7.58	7.03	2.28	2.40	5.70	6.00
W.42.4	3.05	2.40	7.63	6.00	2.11	2.06	5.28	5.15
average	3.09		7.73		2.26		5.66	
sd	0.60		1.50		0.40		1.00	
max.	4.68		11.70		3.56		8.90	
min.	1.85		4.63		1.47		3.68	

APPENDIX G.2: DRYING TEST RESULTS

Kiln Dried Shrinkage

Sample	Shrinkage After Drying (%) Rad.	Tan.	Vol.	Shrinkage After Steaming (%) Rad.	Tan.	Vol.
N.4a -3	1.45	3.26	4.71	1.54	2.88	4.42
N.4a -4	1.22	4.15	5.37	1.31	3.82	5.13
N.4b.1 -3	1.36	3.77	5.13	1.76	3.57	5.34
N.14 -3	1.94	3.22	5.16	1.55	3.22	4.77
N.14 -4	1.92	2.76	4.67	1.75	2.74	4.49
N.42 -3	2.03	5.53	7.56	2.10	3.59	5.69
N.42 -4	2.24	3.50	5.73	2.22	3.36	5.58
S.4a -3	1.80	3.95	5.75	1.96	4.02	5.98
S.4a -4	1.64	4.10	5.74	1.46	3.88	5.33
S.9 -3	2.16	4.64	6.80	2.20	4.51	6.70
S.14 -3	1.77	4.34	6.11	1.74	4.17	5.91
S.41 -3	2.56	3.67	6.23	2.44	3.74	6.18
S.41 -4	2.43	3.42	5.85	5.56	3.40	8.96
N.4b.1 -4			6.03			5.73
N.4b.2 -3			5.41			5.42
N.4b.2 -4			5.43			5.31
S.4b.1 -3			5.56			6.09
S.4b.2 -3			5.60			5.62
S.4b.1 -4			5.45			5.61
S.4b.2 -4			5.62			5.79
S.9 -4			7.07			7.07
S.14 -4			6.42			6.04
S.42 -3			5.39			5.26
S.42 -4			5.01			5.03
average	1.89	3.87	5.74	2.12	3.61	5.73
sd	0.40	0.71	0.70	1.09	0.50	0.92
max.	2.56	5.53	7.56	5.56	4.51	8.96
min.	1.22	2.76	4.67	1.31	2.74	4.42

Air Dried Shrinkage

Sample	Shrinkage After Drying (%)			Shrinkage After Steaming (%)		
	Rad.	Tan.	Vol.	Rad.	Tan.	Vol.
N.4a -1	1.06	3.18	4.24	1.36	3.30	4.66
N.4a -2	0.99	3.08	4.07	1.19	3.15	4.34
N.4b.1 -1	1.70	3.33	5.03	1.85	3.40	5.25
N.14 -2	0.44	1.09	1.53	1.09	3.13	4.21
N.41 -1	1.42	3.39	4.81	2.01	4.19	6.19
N.41 -2	0.20	1.11	1.31	1.94	3.92	5.87
N.42 -1	0.56	1.49	2.05	2.28	3.92	6.20
S.4a -1	1.39	3.72	5.11	2.09	4.06	6.15
S.4a -2	1.47	3.68	5.15	2.52	3.56	6.08
S.4b.2 -1	1.41	3.43	4.84	1.87	3.43	5.30
N.4b.1 -2			4.74			4.77
N.4b.2 -1			4.41			4.69
N.4b.2 -2			4.38			4.88
N.14 -1			1.57			5.06
N.42 -2			1.56			5.82
S.4b.1 -1			4.21			4.82
S.4b.1 -2			4.85			5.48
S.4b.2 -2			4.52			5.12
S.9 -1			5.17			5.92
S.9 -2			3.98			5.49
S.14 -1			1.52			5.13
S.14 -2			1.18			5.15
S.42 -1			2.66			6.38
S.42 -2			1.79			6.27
average	1.06	2.75	3.53	1.82	3.60	5.38
sd	0.51	1.07	1.51	0.47	0.39	0.65
max.	1.70	3.72	5.17	2.52	4.19	6.38
min.	0.20	1.09	1.18	1.09	3.13	4.21

APPENDIX H: CLIMATE PROFILES FOR NEW ZEALAND MODEL

	Chinese Data (16 sites)			NZ Data (2 sites)	
	Min.	Mean	Max.	Min.	Max.
Temperature (°C)					
Mean monthly	15.3	17.6	**21.8**	**12.8**	13.2
Min monthly *	**0.1**	6.6	**14.8**	2.9	5.8
Max monthly *	**20.2**	27.7	**29.5**	21.6	23.3
Range	**10.6**	21.1	**28.8**	15.8	20.4
Seasonality	**0.6**	1.2	**1.8**	1.2	1.6
Driest quarter *	**3.3**	9.3	**17.4**	17.0	17.3
Wettest quarter *	20.0	25.4	**27.7**	**8.9**	10.4
Solar radiation (MJ m^{-2} day^{-1})					
Mean daily	14.8	17.9	**20.1**	**12.5**	13.2
Min monthly *	8.4	11.3	**16.0**	**5.1**	5.8
Max monthly *	21.7	25.9	**28.5**	**20.4**	21.2
Range	**10.3**	14.6	**17.2**	15.3	15.4
Seasonality	**0.5**	0.8	1.1	**1.2**	1.2
Driest quarter *	**9.5**	12.4	**18.9**	15.7	16.3
Wettest quarter *	18.4	22.6	**25.3**	**5.9**	6.5
Rainfall (mm)					
Mean annual	**829**	1370	**2100**	1395	1738
Min monthly *	**2**	35	71	98	**112**
Max monthly *	**119**	232	**370**	135	177
Range	87	197	**323**	**37**	65
Seasonality	1.3	1.8	**3.1**	0.8	**0.5**
Driest quarter *	**30**	127	239	302	**360**
Wettest quarter *	**300**	616	**965**	395	512

Values in bold represent combined climate profile for *C. lanceolata* used to obtain predicted sites in New Zealand.

* Indicates key variables used in the reduced dataset.

APPENDIX I: LIST OF ABBREVIATED VARIABLES USED IN EXPERIMENTS

Chapter IV

GV	Germination Value		
LAT	Latitude (°N)	LON	Longitude (°E)
ALT	Altitude (m)	MAT	Mean Annual Temperature (°C)
MCT	Mean January Temperature (°C)	MWT	Mean July Temperature (°C)
TSM	Temperature Sum	MAR	Mean Annual Rainfall (mm)
MAS	Mean Annual Sunshine (hours)	FFD	Frost Free Days
BB_t	Terminal Bud Burst	BB_l	Lateral Bud Burst
BS	Bud Set	FD	Frost Damage

Chapter V

F	Frequency of Fast Allele	S	Frequency of Slow Allele
VS	Frequency of Very Slow Allele	H	Expected Heterozygosity
A	Mean Number of Alleles per Locus	P	Percentage of Polymorphic Loci
D	Nei's (1978) Genetic Distance	I	Nei's (1978) Genetic Identity
G_{st}	Nei's (1973) Relative Measure of Differentiation		

Chapter VI

L	Leaf Weight (g)	R	Root Weight (g)
S	Stem Weight (g)	T	Total Weight (g)
C	Cotyledon Weight (g)	H_t	Total Height (mm)
H_s	Cotyledon to Apex Height (mm)	N_l	Number of Leaves
L_l	Length of Longest Leaf (mm)	A_l	Leaf Area (mm^2)
A_l:T	Leaf Area: Total Weight Ratio	L:T	Leaf Weight: Total Weight Ratio
A_l:L	Leaf Area: Leaf Weight Ratio		
RGR	Relative Growth Rate (g g^{-1} day^{-1})	$ß_1$ = RGR	
PS	Net Photosynthesis (µmol m^{-2} s^{-1})		

Chapter VII

RGR	Relative Growth Rate (g g^{-1} day^{-1})		
L	Leaf Weight (g)	R	Root Weight (g)
S	Stem Weight (g)	T	Total Weight (g)
lnL	Log_e(Leaf Weight)	lnR	Log_e(Root Weight)
lnS	Log_e(Stem Weight)	lnT	Log_e(Total Weight)
S:T	Stem Weight: Total Weight Ratio	S:L	Stem Weight: Leaf Weight Ratio
S:R	Stem Weight: Root Weight Ratio	R:L	Root Weight: Leaf Weight Ratio

R:T	Root Weight: Total Weight Ratio	L:T	Leaf Weight: Total Weight Ratio

Chapter VIII

H	Frost Hardiness

Chapter IX

SM	Seedling Mortality (%)	D%	Percentage Diameter Growth
L_o	Old Leaf Weight (g)	L_n	New Leaf Weight (g)
S_o	Old Stem Weight (g)	S_n	New Stem Weight (g)
R	Root Weight (g)	T	Total Weight (g)

R:LS	Root Weight: Above Ground Weight Ratio
R:T	Root Weight: Total Weight Ratio
L:T	Leaf Weight: Total Weight Ratio
S:T	Stem Weight: Total Weight Ratio
LS_n:T	New Above Ground Weight: Total Weight Ratio
LS%	Percentage of New Above Ground Growth (%)
PS_{stress}	Net Photosynthesis of Stressed Seedlings ($\mu mol\ m^{-2}\ s^{-1}$)
$PS_{recovery}$	Net Photosynthesis of Seedlings Watered to Field Capacity ($\mu mol\ m^{-2}\ s^{-1}$)
SR_{stress}	Stomatal Resistance of Stressed Seedlings ($s\ cm^{-1}$)
$SR_{recovery}$	Stomatal Resistance of Seedlings Watered to Field Capacity ($s\ cm^{-1}$)
PD_{stress}	Pre-dawn Plant Moisture Stress of Stressed Seedlings (bars)
$PD_{recovery}$	Pre-dawn Plant Moisture Stress of Seedlings Watered to Field Capacity (bars)
MD_{stress}	Mid-day Plant Moisture Stress of Stressed Seedlings (bars)
$MD_{recovery}$	Mid-day Plant Moisture Stress of Seedlings Watered to Field Capacity (bars)
M-P_{stress}	Mid-day - Pre-dawn Differential of Stressed Seedlings (bars)
M-$P_{recovery}$	Mid-day - Pre-dawn Differential of Seedlings Watered to FC (bars)

Chapter X

L	Leaf Weight (mg)	R	Root Weight (mg)
S	Stem Weight (mg)	T	Total Weight (mg)
D	Diameter (mm)	L:T	Leaf Weight: Total Weight Ratio
S:T	Stem Weight: Total Weight Ratio	L:S	Leaf Weight: Stem Weight Ratio
L:R	Leaf Weight: Root Weight Ratio	S:R	Stem Weight: Root Weight Ratio

N	Above Ground Plant Tissue Concentration of Nitrogen (%)
P	Above Ground Plant Tissue Concentration of Phosphorous (%)
K	Above Ground Plant Tissue Concentration of Potassium (%)
Ca	Above Ground Plant Tissue Concentration of Calcium (%)
Mg	Above Ground Plant Tissue Concentration of Magnesium (%)

Chapter XI

L	Leaf Weight (g)	R	Root Weight (g)
S	Stem Weight (g)	T	Total Weight (g)
L:T	Leaf Weight: Total Weight Ratio	L:R	Leaf Weight: Root Weight Ratio
R:T	Root Weight: Total Weight Ratio	D	Basal Stem Diameter (mm)
H	Height Above Ground (mm)	B	Number of Branches
BB	Percentage of Bud Burst (%)		

Chapter XII

LP	Terminal Bud Primordia	OL	Previous Season's Leaves
LP/OL	Estimation of Predetermined Growth	SB	Sub-terminal Bud

Chapter XIII

Lon	Longitudinal Shrinkage (%)
Rad	Radial Shrinkage (%)
Tan	Tangential Shrinkage (%)
Vol_{trt}	Volumetric Shrinkage After Drying (%)
Rad_{trt}	Radial Shrinkage After Drying(%)
Tan_{trt}	Tangential Shrinkage After Drying(%)
Vol_{rec}	Volumetric Shrinkage After Steaming (%)
Rad_{rec}	Radial Shrinkage After Steaming(%)
Tan_{rec}	Tangential Shrinkage After Steaming(%)
MOE	Modulus of Elasticity (GPa)
MOR	Modulus of Rupture (MPa)
FSPL	Fibre Strength at the Proportional Limit (MPa)
MCS	Maximum Compression Strength (MPa)
CSPL	Compressive Strength at the Proportional Limit (MPa)
MSS	Maximum Shear Strength (MPa)

Chapter XIV

Ti	Tip Browse	Br	Branch Browse
St	Stem Browse	No	No Browse
Se	Severe Bark Damage	Mo	Moderate Bark Damage
Li	Light Bark Damage		